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FOREST DIVERSITY AND CONSERVATION IN THE WESTERN AMAZON BASED ON TREE INVENTORY AND REMOTE SENSING DATA

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by

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Dedication

To my loved ones and the Amazon.

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FOREST DIVERSITY AND CONSERVATION IN THE WESTERN AMAZON BASED ON TREE INVENTORY AND REMOTE SENSING DATA

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This dissertation contributes to debates in conservation biogeography by examining the spatial heterogeneity of local and regional tree diversity feature using ground and remotely sensed data, and by taking approaches to design a spatially explicit landscape zonation map for future conservation planning in western Amazon, one of the most biodiverse regions on Earth. Fine scale tree diversity and conservation-related studies took place in tropical rainforests in southeastern Ecuador, whereas coarse scale tree diversity research was conducted using data from eastern Ecuador and northern Peru.

The lack of species assemblages within three 1-ha tree inventory plots in southeastern Ecuador and the weak correlations with biophysical environment implied that neutral processes may contribute to species diversity. In contrast, differences in species assemblages between plots corresponded to relative geographic locations of the plots, indicating that geographic distance or dispersal limitation may play an important role influencing diversity patterns at a regional scale.

Species of high local abundance was found in 1-ha tree inventory plots in western Amazon. Changes in density of locally abundant species between western and eastern plots indicated that some species may have limited distributions. Shifts in species dominance and the significant relationship between floristic variation and geographic distances between plots implied dispersal limitation. Variation in rainfall showed significant relationship with species composition. Therefore, dispersal limitation and precipitation seasonality are potentially the most significant factors that contribute to spatial differences in tree diversity in western Amazon.

Characteristics of canopy shadows and palm stem density based on fine-resolution aerial photographs were characterized as exploratory analyses to extract alpha and beta diversity features using remotely sensed data. A zonation map design using multispectral habitat classification and other remote sensing data performed well in its spatial arrangement when potential indigenous land use was integrated. Based on the results of analyses for conservation biogeography, this dissertation concludes that local and regional tree diversity may be influenced by dispersal limitation and seasonality, and that the application of remote sensing for biodiversity conservation is feasible in very species-rich forests.

Table of Contents

List of Tables

List of Figures

List of Illustrations

Chapter 1: Introduction

Research in conservation biogeography entails two fundamental elements: understanding biodiversity patterns and applying biodiversity studies towards conservation (Whittaker 2005). In particular, biogeographers have always striven to understand why tropical regions harbor such great species diversity. To this day, proposing mechanisms and testing hypotheses for explaining tropical species diversity remains one of the most prominent but least understood areas of study in biogeography. Some of the most widely accepted hypotheses postulate that plant productivity-related variables, especially measures in involving water and energy features, facilitate the accumulation of biomass and population in the tropics, which as a result support great plant diversity (Allen et al. 2002, Hawkins et al. 2003, Kreft and Jetz 2007). The longer growing and rainy season supports more species with a great variety of functional types. Thus, the climate towards the equator could support greater speciation or could support more tropical species (ter Steege et al. 2003, Mittelbach et al. 2007). Another argument explaining high tropical plant diversity states that the majority of tropical trees may be habitat specialists (Pitman et al. 2001, Kreft and Jetz 2007). These mechanisms substantiate the idea that a tropical tree diversity study should directly or indirectly tie together data on climate, water-energy balance, and biotic/abiotic habitat heterogeneity. This approach would be useful for examining how these factors interplay in understanding the spatial heterogeneity of local tree diversity and in interpreting regional tree diversity patterns.

One pitfall that biogeographers often encounter is the lack of diversity data in remote areas and an unbalanced sampling effort between remote areas vs. areas with easy access. Due to limited accessibility, documenting tropical tree species diversity patterns

and characterizing biodiversity features using remote sensing data provide a more efficient approach (Turner et al. 2003, Cayuela et al. 2006, Saatchi et al. 2008). In particular, since plant species richness is a fundamental element of diversity at the community and regional scales, attempts may be made to predict species richness and its spatial heterogeneity using spectral heterogeneity in remote sensing images as a proxy. Use of spectral variance of satellite images may help predicting species richness (Rocchini et al. 2004). This hypothesis can be tested by comparing the relationship between the spectral heterogeneity in multispectral images and species richness in inventory plots of different size (Rocchini 2007a, b). Remote sensing-derived vegetation indices, species richness or diversity, or patch pattern metrics (e.g. patch diversity, connectivity, and shape complexity) may display correlations with field-based species diversity, and hence give further insights on mapping and predicting diversity patterns (Rocchini et al. 2004, Rocchini 2007a, b).

Remote sensing studies often examine patterns in the biotic/abiotic environment and in regards to scale (Quattrochi et al. 2003). Scale impacts the discernible patterns within the fine/local and coarse/regional landscape units (Turner et al. 2001). Hence, spatial scale refers to the spatial dimensions in different imagery resolutions (pixel size) and extents (boundaries of the study region) (Odum 1994). Biogeographers with remote sensing interests should consider detecting multiscale ecological patterns by using remote sensing analyses, as well as examining if vegetation patterns at one scale explain the patterns at other scales (Turner 2005). Field data and high-resolution remote sensing data contribute to understanding local diversity patterns. If such information at the local scale is discernible at the regional scale or vice versa, regional (local) patterns of habitat heterogeneity and species richness may be detected based on local (regional) biological and habitat data. In addition, linking local and regional species diversity patterns by

integrating field and remote sensing data should facilitate obtaining fundamental biodiversity knowledge in remote areas as the basis for future conservation plans.

Biodiversity conservation one of the biggest challenges that modern society is facing (Dirzo and Loreau 2005). There are urgent needs to integrate biological and social disciplines for incorporating biodiversity conservation into global mainstream policies. Thus, biodiversity conservation has evolved into a "biodiversity science" (Dirzo and Loreau 2005). Remote sensing contributes to the biodiversity science by expanding the array of knowledge used in conservation. Dirzo and Loreau (2005) further recognized that remote sensing-based analyses have allowed substantial progress towards understanding biodiversity distribution and change.

CONCEPTUAL APPROACHES

This dissertation embodies elements from disciplines of: 1) conservation biogeography and biodiversity science, and 2) biodiversity conservation and systematic conservation planning. While the theoretical components are based on mechanisms that explain biodiversity patterns, the methods are based on examining patterns expected due to some of the mostly debated mechanisms. In addition, remote sensing data and analysis are used as tools to explore arrays that facilitate understandings of landscape features that represent biodiversity characteristics. The research questions examine tree diversity patterns and habitat heterogeneity at local and regional scales by employing both field and remote sensing-based approaches. Ultimately, this study utilizes characterized vegetation types to assist in creating landscape zonation maps for a remote tropical site for future conservation planning.

Conservation biogeography and biodiversity

Conservation biogeography

Biogeographers may view biodiversity with an ecological orientation that relates shifts in species spatial distribution to the biophysical environment that determines species ranges (Young et al. 2003). With a growing concern of degrading habitats and decreasing species diversity, biogeography studies began to examine how biodiversity shifts in space and time in the changing ecosystems and the importance to conserve biodiversity at local, regional, and global scales (Grehan 1995). Conservation biogeography is defined as the application of biogeographic theories and analyses concerning the distribution dynamics of taxa and the conservation of biodiversity (Whittaker 2005). It involves applications of biogeography principles and analyses of problems regarding conservation (Richardson and Whittaker 2010). Conservation biogeographers may identify ecoregions with the biogeographically representation approach (Dinerstein et al., 1995), target places that are rich in species and under threats using a hotspot approach (Myers et al., 2000), or combine both hotspot and representation approaches to define 200 global ecoregions (Olson and Dinerstein, 1998). The initial step of understanding species diversity patterns must take place before any of these approaches can be employed. More specifically, aspects that conservation biogeography takes into consideration include species distribution modeling, conservation priority assessment, integration of information from disparate sources, biological invasion, and responses to climate change (Richardson and Whittaker 2010).

Further insights on these aspects have been given since the formal definition of conservation biogeography. Franklin (2010) proposed that species distribution modeling can link landscape disturbance, habitat suitability, and dynamics of habitats and population, in order to allow combined impact of climate change and land cover

dynamics on species to be predicted in a multi-modeling framework. By considering conservation planning in a network basis, Cumming et al. (2010) defined challenges of network-based conservation as cross-scale linkages in ecosystems, capturing dynamics of ecosystem networks, and integrating analysis of social and ecological networks. Since conservation biogeography studies often require considerable amount of datasets collected over large spatio-temporal scales, Devictor et al. (2010) believed that citizen science programs that allow datasets to be collected by general public can be highly valuable in providing technical advances and in promoting reconnection between people and nature. Some of the core challenges exist for conservation biogeographers, such as testing theories in conservation biogeography, quantifying species loss and extinction, elucidating patterns of invasion, and characterizing features of biodiversity crisis (Olden et al. 2010).

"Why are there so many species in the tropics?"

Conservation biogeographers ask a fundamental question regarding what contributes to biodiversity patterns. Likewise, *Science* magazine in 2005 asked "What determines species diversity?" and considered it as one of the 25 major research themes facing science over the next quarter-century (July 1, 2005). Furthermore, researchers still strive to understand why tropical regions harbor greater species diversity compared to higher latitudes. Geographers and ecologists more than two centuries ago began to notice a trend in increasing species diversity towards the equator (Lomolino et al. 2004). Lomolino et al. (2006) organized more than 30 diverse explanations for this natural mystery into categories consisting of null models, biotic interactions and processes, abiotic or environmental factors, and fundamentally integrative processes. In this

dissertation I examine if local and regional tree diversity patterns might support any of these theories.

Species diversity and composition in relation to spatial heterogeneity has always been one core of biogeographic studies. Some of the following hypotheses may explain the captivating species diversity in the tropics (Pianka 1966): 1) a time theory that the latitudinal gradient reflects the historical glaciation and climatic perturbation in the temperate zones, 2) the greater spatial heterogeneity in the tropics, 3) more competition and resource specialization in the tropics, 4) the lower pressure of predation, 5) climatic stability, and 6) the higher productivity. I begin the following literature review with null models of species diversity.

Colwell and Hurtt (1994) claimed that random placement of species' distribution ranges between geographically constraining "domains" (e.g. the continents of the New World) causes the highest overlap of species ranges towards the middle of the domains, resulting in the greatest species richness towards the mid-domain. Excluding any direct environmental or evolutionary factors, this stochastic phenomenon of the mid-domain effect (MDE) may contribute to the latitudinal gradient in tree diversity (Colwell and Lees 2000). A critical problem mid-domain effect faces is that it does not fully exclude the environment when setting domain boundaries. Such fundamental failure in constructing a "null" model might explain the low correspondence between predicted vs. observed latitudinal diversity patterns in a study by Bokma and Monkkonen (2001).

Hubbell's unified neutral theory of biodiversity is a recent theory that challenges the traditional theories explaining tropical biodiversity. The fundamental assumption made is that all trees are competitively equivalent in their rates of birth, death, dispersal, and speciation (Hubbell 2001). This implies that biodiversity arises at random and is associated with stochastic events, as each species follows a random walk (McGill 2003).

Processes such as extinction and speciation that control the origins and interactions of populations at the individual level are stochastic (Alonso et al. 2006). The factors that influence random extinction, speciation, and population density may indirectly favor higher species diversity in the tropics. Nevertheless, Pitman et al. (2001) rejected Hubbell's null model after finding non-random distribution of common species that are shared between two Amazonian forests in Ecuador and Peru, suggesting that at least the dominant species do not occur at a random walk. Furthermore, using this theory to predict species diversity does not directly provide explanations for tropical species diversity (Turner and Hawkins 2004).

Turner and Hawkins (2004) asked if greater number of niches in the tropics results in higher species diversity or greater species diversity forms more diversified niches. This necessitates explanation about how species diversity is imposed by habitat heterogeneity and niche width. Niche theory postulates that certain suites of environmental factors limit species distribution and are essential for species' life cycles (Hutchinson 1957). Tropical species are more specialized in their environment than species at higher latitudes (Greenwood 2001); environmental suites (i.e. niches) tend to be narrower for species in the tropics than in the temperate regions. Therefore, a greater number of more niche-specialized species can coexist in the tropics (Brown and Gibson 1983). Various versions of the niche assembly theory suggest that 1) tropical species have narrower niche space than temperate species given the same total resource, 2) tropical species share resource space to a greater extent given the same total resource space and niche size, and 3) tropical areas have a larger resource space given the same niche size (Turner and Hawkins 2004). A greater niche diversification may also be a reflection of greater habitat (e.g. canopy strata) diversity and biological spatial heterogeneity. The more vertically and horizontally heterogeneous habitats in the tropics lead to a more

complex spatial mosaic of species distribution and patchiness than in the temperate regions. This allows more species to coexist (MacArthur et al. 1966, MacArthur 1972). For example, Gentry (1988) observed that tropical tree communities show discernible patterns in species richness and the composition of at least families is to some extent predictable from environmental parameters. In addition, interspecific competition also plays a role in niche differentiation. The competing species can be driven into different patterns of resource use or different niches. This process allows different species to partition certain resources and therefore, species coexistence is obtained through the differentiation of realized ecological niches (Diamond 1978, Connell 1983). My dissertation examines the potential environmental niche differentiation, but niche partitioning driven by interspecific competition is not examined due to the lack of temporal data required for such analysis.

In addition, the area hypothesis states that tropical regions occupy a greater portion of the earth's surface and this is what leads to higher population numbers, larger species ranges, and a lower chance of extinction (Terborgh 1973, Rosenzweig 1995). A larger area positively affects speciation if larger species ranges can expose species to greater environmental heterogeneity along the latitudinal gradient (Rosenzweig 1995). However, the often ignored paradox is that increasing species diversity may reduce the population size and species ranges that tropical regions can host (Chown and Gaston 2000). Chown and Gaston (2000) also pointed out that other mechanisms modulating the area model may obscure the area effect itself. This includes the influence of productivity on species richness and the difference in mechanisms promoting species ranges in the tropics vs. in the higher latitude. Furthermore, ter Steege et al. (2000) pointed out that the area hypothesis may not contribute to difference in species diversity between different regions of the Amazon.

An older theory states that over evolutionary time periods, the climate and older environment in the tropics may allow species to have more time to disperse and colonize to suitable habitats. Species are also able to adapt to and specialize to the more predictable environment and accumulate species richness (Wallace 1878, Fischer 1960, Pianka 1966). The longer species accumulation time and environmental history and a higher speciation rate in the tropics than at higher latitude should promote older species in average and greater variation in species age (Mittelbach et al. 2007). Stropp et al. (2009) argued that regional diversity is correlated with paleo-climatic stability, as represented by the age of geological formation. Hoorn et al. (2010) further stated that uplifts from the Andes reconfigured drainage patterns, created a vast influx of sediments into the Amazon basin, and developed an edaphic mosaic that became rich in species. At the evolutionary time scale, speciation and extinction rates influenced by the area effect may also couple with this climate stability-time effect to generate the current diversity gradient for tree species (Fine and Ree 2006). Hence, Mittelbach et al. (2007) suggested that the key to understand the gradient of diversity lies in exploring the mechanisms responsible for the higher speciation rates in the tropics.

Plant water-energy balance governs productivity at a global scale and is measured by the amount of water driven through ecosystems through thermal energy. Both water and solar energy decline from the tropics to the poles and therefore, the productivity that accounts for plant growth and biomass shows a latitudinal gradient (Turner and Hawkins 2004). The tropics should have higher species diversity since there are more individuals in the warmer and more humid environment (Wright 1983, Currie and Paquin 1987). This water-energy hypothesis (a.k.a. the productivity hypothesis) makes testable predictions. This includes that species diversity should present strong correlations with measures directly related to productivity such as actual evapotranspiration (AET) or potential

evapotranspiration (PET) (Turner and Hawkins 2004). Productivity, water availability, or combined measures of water and energy in particular explain the most spatial variation in species richness at low latitudes, whereas temperature or PET explain the most variation at high latitudes (Hawkins et al. 2003).

A meta-analysis that generalized the latitudinal gradient diversity patterns performed by Hillebrand et al (2004) using a large pool of published literature revealed that the change in species richness with latitude does not falsify or directly support any single hypothesis. However, a combination of water-energy and climate factors most likely contributes to the latitudinal species gradient. I agree that productivity and its climatic proxies play important roles in regulating the latitudinal diversity gradient. Furthermore, I also agree that no single variable can fully account for species diversity (Turner and Hawkins 2004). Multiple non-mutually exclusive hypotheses including climate stability and habitat heterogeneity may likely act synergistically with the dominant water-energy factor to affect the latitudinal tree diversity gradient (Kreft and Jetz 2007).

A model created by Allen et al. (2002) quantitatively predicts that species diversity increased with environmental temperature along a latitudinal gradient. This result is consistent with the findings of a meta-analysis that water and energy variables provide a strong explanation for global diversity gradient (Hawkins et al. 2003). In another meta-analysis, PET is one of the core predictors that explain variation in global species richness and a full account of the latitudinal gradient in species richness (Kreft and Jetz 2007). Consequently, I propose that plant productivity-related variables, especially measures in water and energy features, facilitate the accumulation of biomass and population of individual species in the tropics that support greater tree diversity.

Qian and Ricklefs (2007) found that at a continental scale both geographic distances and climatic differences between latitudinal zones in North America explain satisfactorily the variation using the Jaccard index of species similarity of vascular plants. Temperature, precipitation, and evapotranspiration as a result account for latitudinal gradients in beta diversity, at least in North America. Likewise, in another study the number of wet days per year appears to be one of the important predictors that explain variation in global species richness and the latitudinal gradient in species richness (Kreft and Jetz 2007). The climate-controlled latitudinal gradient is profound even within the Neotropical region. A spatial model that predicts tree alpha diversity in the Amazon detects high negative correlations between dry season length and the maximum Fisher's alpha diversity, which peaks at the equator (ter Steege et al. 2003). The longer growing and raining season harbors more species with a great variety of functional types. At an evolutionary scale, observations that the age of latitudinal regions shows positive correlations with species diversity and that temperate taxa are often younger than tropical taxa underpin the argument that the older tropical climate has allowed more opportunities for diversification (Mittelbach et al. 2007).

Environmental habitat heterogeneity is the third mechanism and it plays a significant role in explaining global patterns of vascular plant diversity (Kreft and Jetz 2007). Based on a study in in two upper Amazonian forests, Pitman et al. (2001) concluded that the majority of tree species in western Amazon may be habitat specialists that are highly sensitive to environmental heterogeneity. This determines the spatial extent of species dominance. The area covered by a small set of dominant species is large when environmental heterogeneity is low. This finding validates the niche theory that predicts overlaps between species niche requirements (i.e. niche space) and local environmental conditions (i.e. resource space) control local species richness (Turner and

Hawkins 2004). I suggest that environmental habitat heterogeneity controls niche width and the extent to which a few species dominate the landscape and therefore governs the gradient in tree diversity.

These mechanisms and their respective evidences substantiate the idea that a tree diversity gradient study should tie data together on climate, water-energy balance, and biotic/abiotic habitat heterogeneity. This idea may be useful for examining how these three factors interplay in expounding the spatial heterogeneity of local tree diversity and in interpreting global tree diversity patterns. Different mechanisms could have complex and synergistic effects on underlining the maintenance of species diversity, as Leigh et al. (2004) pointed out that trees face trade-offs in suitability for different habitats, climatic conditions, disturbance regimes, and resistance to pests. In the following section I integrate different opinions in regard to tree diversity research and hope to shed light on exploring future challenges and opportunities.

Challenges and opportunities: conceptualizing a multi-scale hierarchy

Understanding biodiversity patterns in conservation biogeography research necessitates dissecting biodiversity features from a scale-based foundation. From a geographic perspective, processes that regulate diversity appear in a spatio-temporal hierarchy from local to landscape, regional, and continental levels (Hill and Hill 2001). One common definition of biodiversity tightly links species diversity to spatial scales. Whittaker (1977) augmented the tiered diversity framework by setting out a hierarchy that encapsulates points, alpha diversity, beta diversity, and gamma diversity. My dissertation aims to examine alpha and beta diversity elements and distribution patterns based on measures obtained from ground and remotely sensed data. Whittaker (1972) defined alpha diversity as a within-habitat number of species and defined beta diversity

as a measurement of similarity, ratio of species richness, or species gain and loss across communities along an environmental gradient. In addition, alpha diversity can also represent niche spacing and overlap among species besides meaning the local number of species (MacArthur 1972).

Beta diversity can also be the inverse of the average number of habitats occupied by each species within a larger region because habitat variety contributes to distinguishing regional species (Schluter and Ricklefs 1993). Tuomisto (2010a, b) argued that true beta diversity is partitioned into the effective number of species per sampling unit. Other popular beta diversity measures include regional-to-local diversity ratio, two-way diversity ratio, absolute effective species turnover, Whittaker's effective species turnover, proportional effective species turnover, and regional entropy excess and regional variance excess (Tuomisto 2010a, b). These different measures emphasize ecological properties that include the degree of emphasis on presence/absence vs. relative abundance information (Anderson et al. 2011). Anderson et al. (2011) also suggested that using multiple beta diversity measures in concert can uncover the underlying nature of diversity patterns.

Whittaker (1972) defined gamma diversity as a multiplicative function of alpha and beta diversity, as did Cox and Ricklefs (1977) with an expansion of adding the total sample dimension into the equation. Cody (1993) referred to species replacement over distance and across physical environment within a habitat type as the gamma component of regional diversity. An interest in global biodiversity patterns has lead recent studies to examine gamma diversity among different regions or total species diversity across regional scales (Ojo and Ola-Adams 1996, Webb and Peralta 1998).

Alpha diversity may be caused by micro-environmental variables whereas beta diversity that is controlled by habitat heterogeneity variables. Governed by climate and

water-energy dynamics, gamma diversity may provide a general scheme for understanding variation in landscape and local diversity. Whittaker et al. (2001) only proposed a macro-ecological top-down view to create a climate-based model for predicting species diversity from regional to local scales (derived from Brown 1995). However, I argue that the bottom-up insight suggested by Tilman (2000) should share equal attention and interests by biogeographers when studying tree diversity latitudinal gradients. Tilman (2000) suggested that the mechanisms most relevant to ecosystem functioning are also those that maintain diversity. It is from interspecific interactions at the local scale that diversity is expected to impact ecosystem processes. In addition, biogeographers should not ignore a temporal hierarchy (from short to long term scales) of dominant processes that control evolutionary patterns and species diversity (Whittaker et al. 2001).

Yet, the difficulties of integrating major tree diversity controlling mechanisms into a species diversity study still exist conceptually, practically, statistically, and analytically. This is true both in a spatial top-down or bottom-up hierarchy and in the context of temporal evolutionary hierarchy. In my opinion, how biogeographers achieve such integration remains the biggest challenge in the future research of tree diversity studies.

Challenges and opportunities: challenges in biodiversity studies

Understanding biodiversity patterns requires examinations of the complex interactions between the environment and biodiversity features. The term "biological diversity" was first mentioned in 1968, first introduced to the science community in 1980, and first used in the abbreviated term "biodiversity" in a publication in 1988 (Dasmann 1968, Lovejoy 1980, Wilson 1988). Biodiversity could represent the total

variability and complexity at every level of structural, taxonomic, and functional organization inside the biological realm (Takacs 1996). Ecological diversity studies originated in the 1950s-1960s from the idea that each species demonstrates individual responses to environmental gradients. This causes variation in species abundance and composition (Veech et al. 2002). The early biodiversity studies demonstrated that species distribution is associated with environmental gradients, habitat specialization, and forest fragmentation (Sombroek 2000, ter Steege et al. 2000).

Since the establishment of a large permanent plot in Barro Colorado Island, Panama in 1980 (Condit 1998), multiple 1-ha plots have become the standard sampling design for ecological and biogeographic studies of tropical tree communities (e.g. Condit et al. 2002, Duivenvoorden et al. 2002). Results of these inventories have often revealed that local or regional tree diversity is associated with habitat heterogeneity and physical environmental gradients (Duivenvoorden 1995, Duque et al. 2003, Phillips et al. 2003). Variation in tree species diversity across habitats has indicated complexity in determining critical habitats based on species abundance, geographic range and habitat specialization (Terborgh and Andresen 1998, Pitman et al. 1999, Pitman et al. 2002).

Long-term ecological studies in 1-ha plots have elucidated and predicted the dynamics of forest stand structure, productivity, regeneration, mortality and species composition (Lewis et al. 2004, Phillips et al. 2004, Muller-Landau et al. 2006). Species adaptation and interaction perspectives have also explained the mechanisms that cause spatial aggregation and clustering of tree species (Chave 2001, Plotkin et al. 2002). Unfortunately, limitations of sampling 1-ha plots exist for tropical forests. First, field inventory is time consuming, labor intensive, and costly. Second, the spatial relationships among tree species documented in sampled 1-ha plots may only partially explain the species composition at the regional scale (Plotkin and Muller-Landau 2002). Third, 1-ha

plots or transects in the region do not provide sufficient samples in order to examine the spatial heterogeneity of species diversity.

Researchers have considered species diversity patterns influential in terms of affecting ecosystem processes at large spatial and temporal scales (Hooper et al. 2005). Hence, biodiversity conservation acts as a key step in maintaining species interactions, ecosystem functioning, and sustainable natural resource management (Johnson 1993). Nevertheless, most previous studies have only examined local or regional diversity and its complex associations with the physical environment. A relatively novel approach is to use inventory data to estimate large-scale tree diversity patterns and ultimately identify conservation prioritization areas to maximize the efficiency of systematic conservation planning and the use of tree diversity data (Sarakinos et al. 2001, Sarkar and Margules 2002). Remote sensing data can be integrated with habitat heterogeneity data and then followed by selecting areas that satisfy certain conservation goals in order to facilitate systematic conservation planning (Ferrier 2002). My dissertation research employs the approaches described above by using remote sensing to characterize local and regional diversity patterns for identifying conservation prioritization areas.

Challenges and opportunities: adopting new techniques

Large-scale biodiversity studies underpin regional conservation planning by establishing the foundational knowledge of what and where to be prioritized for conservation. Key issues for guiding future biodiversity research should include refining methods to obtain measures of habitat and regional diversity of poorly known taxa and interpreting mechanisms that control diversity patterns using descriptive analysis and predictable estimates (Sax and Whittaker 2004). Existing meta-analysis studies have used forest demographic and local environmental data (Condit et al. 2006), plant species maps

and geostatistical multipredictor models (ter Steege et al. 2003, Kreft and Jetz 2007), exhaustive statistical resampling and analysis of published literature (Hillebrand 2004), computerized literature and datasets (Hawkins et al. 2003), museum collections and species lists (Qian and Ricklefs 2007), phylogenetic analysis and molecular evolutionary data (reviewed by Mittelbach et al. 2007), and predictive models (Allen et al. 2002). There should also be considerations for other approaches that future research.

Due to limited accessibility of remote areas, estimating species diversity patterns using remote sensing data provides greater efficiency (Turner et al. 2003, Cayuela et al. 2006, Saatchi et al. 2008). I advocate that at the ecological time scale, remote sensing imagery can assist in examining how well climate, water-energy, and habitat heterogeneity explicate diversity patterns in areas with no field inventory records. Measures that are derived from remote sensing data, such as landscape patch pattern metrics (e.g. patch diversity, connectivity, and shape complexity), estimates of biomass and productivity, interpolated climatic, hydrological, and topographic data layers may display strong correlations with field or remote sensing-derived vegetation indices, species diversity index, or richness of species groups.

The challenge that biogeographers need to overcome is the uncertainty of using remote sensing data to detect tree diversity patterns. First, the reliability of using pixel- or textural-derived measures or species diversity estimates as a proxy of species diversity needs to be examined. Second, using different types of remote sensing images from different regions may face issues such as 1) the difficulty to juxtapose diversity or habitat features between fine and coarse resolution images within the same region, 2) the lack of congruent spectral or textural information in different regions, and 3) the differences in detectable spatial heterogeneity at different regions.

Remote sensing has helped to investigate tropical deforestation schemes and classify vegetation types since the 1980s (Westman et al. 1989, Weishampel et al. 1998). Since the 1990s, studies has begun to analyze high-resolution satellite imagery to estimate forest biomass, tree crown and basal area, and tree height (Houghton et al. 2001, Drake et al. 2002, Lefsky et al. 2002a, Clark et al. 2004a). Forest dynamics studies have emerged by quantifying tree mortality and successional changes (Lefsky et al. 2002b, Sanchez et al. 2002, Clark et al. 2004b). Landscape structure indices and derived biodiversity index are often related to field-based measures of species evenness, similarity, and diversity indices (Foody and Cutler 2003, Honnay et al. 2003, Oindo et al. 2003). Furthermore, studies that estimate biodiversity by discriminating tree leaves, crowns, or other taxonomic characters have begun to emerge with the improvement of multispectral resolution of the imagery since the 21st century (Asner et al. 2002a, Read et al. 2003, Clark et al. 2004a, Clark et al. 2005). Similarities in spectral reflectance patterns are highly correlated to the similarity patterns in floristic and edaphic variables in the Amazon in regard to the association between species composition and habitat heterogeneity (Tuomisto et al. 2003a, b). As a result, remote sensing in biodiversity studies has become a powerful tool at local and regional scales (Sanchez et al. 2001, Sánchez-Azofeifa et al. 2003, Clark et al. 2004a).

For instance, Landsat Enhanced Thematic Mapper (ETM+) is one of the most commonly used imageries in tropical vegetation studies. NASA launched the Landsat 7 spacecraft of the ETM+ sensor in 1999, with six multispectral bands (at wavelengths 0.45-2.35 μm), one thermal band (at wavelength 10.4-12.5 μm), and one panchromatic band (at wavelength 0.52-0.9 μm). The spatial resolutions include 15 m (panchromatic band), 30 m (visible, near infrared, and mid infrared bands), or 60 m (thermal band) (NASA 2006). The sensitivity of Landsat ETM+ in detecting landscape features is

evident. In terms of detecting stochastic events, Landsat ETM+ can characterize natural disturbance regimes and quantify patterns of damage/recovery (Asner et al. 2002b, Asner et al. 2004). It also has a high accuracy in separating forest types even in a homogenous forest in the Peruvian Amazon (Salovaara et al. 2005). Spatial estimates of historical land use in the Amazon can be generated when the land classification is fused with ground survey data (Roberts et al. 2003). Landsat ETM+ can also distinguish forest/habitat transition zones (ecotones) and the dynamics of ecotones besides differentiating forest types (Ranson et al. 2004, Bock et al. 2005). Moreover, Landsat ETM-derived spectral and vegetation indices can distinguish forests in different successional stages and demonstrate associations between classified successional stages and forest stand structure or species richness on the basis of forest turnover (Vieira et al. 2003, Arroyo-Mora et al. 2005, Ruiz et al. 2005). In relation to measured vegetation indices, NDVI has explained the variability in leaf area index (LAI) and shown regressional relationships with LAI and plant area index (PAI) in Central America (Kalacska et al. 2005, Jelaska et al. 2006). In addition, NDVI, infrared index (IRI), and mid infrared index (MIRI) based on Landsat ETM+ have demonstrated associations with forest species composition (Feeley et al. 2005).

While Landsat images characterize medium-coarse scale biodiversity features at the landscape, high resolution remote sensing data can describe in greater details the fine-scale characteristics of biodiversity patterns. As an exploratory analysis, my dissertation examines the spatial distribution patterns of canopy shadows and palms using very fine-resolution remote sensing imagery. I use object-based classification, a classification method that has become popular in recent years, to extract canopy shadows from aerial photos. Object-based classification delineates segments of real world objects and considers topological relations among neighboring pixels (Bunting and Lucas 2006,

Hájeck 2006). A few studies have characterized canopy gaps using remote sensing techniques for quantification of forest canopy properties, as the canopy gaps have been well known to play a key role in forest structure and ecological processes (Foody et al. 2003, Koukoulas and Blackburn 2004, Plowes 2005, Asner et al. 2008, Hinsley et al. 2008, Morales et al. 2008). The importance of canopy palms in forest structure, dynamics, and recruitment has been examined in multiple studies (e.g. Farris Lopez 2004, Vormisto et al. 2004, Wang and Augspurger 2004, 2006). My dissertation examines palm distribution in association with canopy shadows in order to complement other palm studies that examined how palms are associated with canopy gaps or general disturbances (Martinez-Ramos et al. 1988, Svenning 1999, Rodriguez-Buritica et al. 2005, Pintaud 2006, Baez and Balslev 2007, Yepes et al. 2010).

Biodiversity conservation and systematic conservation planning

Challenges and crisis for biodiversity conservation

Implementing biodiversity conservation practices requires fundamental understanding of species diversity, threats to biodiversity, and solutions to mitigate the conflict between conservation and development. However, biogeographers often feel that their knowledge of the overall biodiversity on earth is inadequate because a great portion of taxa remains unknown or to be discovered. This is termed the Linnaean shortfall by Brown and Lomolino (1998). It represents a pressing challenge as well as a motivating opportunity for field biologists (Lomolino et al. 2006). Another inadequacy is termed the Wallacean shortfall, which refers to the need of greater knowledge regarding global, regional, and local distributions of certain taxa (Lomolino 2004). Many remote areas in the world remain under-explored and under-collected. Consequently, reliable species

distribution maps that are essential for robust analysis of biodiversity patterns only exist for a fraction of the earth's surface (Whittaker et al. 2005, Davies et al. 2006).

In addition, ecologists have found that global change, including climate and the environmental change has brought considerable impact on ecosystem functioning. Unsustainable land use, massive land conversions, and degradation of natural habitats are some of the global concerns that might harm biodiversity (ter Steege 2010a). Ecologists have identified climate change and dynamics in ecosystem functioning as one of the pressing biodiversity conservation challenges in several discussions (e.g. Dirzo and Loreau 2005, Davies et al. 2006, Miles et al. 2006). Changes in ecosystem functioning, aboveground biomass, forest growth, and stem turnover are partially attributed to deforestation, changes in land use, and habitat degradation (Phillips 1997, Laurance et al. 2002, Baker et al. 2004, Keller et al. 2004, Asner et al. 2005, Nascimento and Laurance 2004).

Thus, habitat loss, degradation, and fragmentation have been considered as some of the most urgent biodiversity conservation problems (e.g. Dirzo and Loreau 2005, Tabarelli et al. 2005, Miles et al. 2006). Deforestation and drastic changes in land use are accountable for a decrease in biodiversity (Messina and Walsh 2001, Laurance et al. 2004, Foley et al. 2005). For example, rapid deforestation and habitat degradation in the tropics result in reduction in habitat heterogeneity. They may precipitate a new wave of tropical species extinction (Laurance 2007). An estimate of species extinction rates in the Brazilian Amazon indicated loss of 20% and 33% of tree species (Hubbell et al. 2008). In addition, a degraded landscape may make the habitats more susceptible to species invasion that ultimately causes decline in biodiversity and the extinction of endemic species (Tabarelli et al. 2005, Davies et al. 2006).

Some scientists may question the feasibility of biodiversity conservation and its potential for success. Their doubts originated from the trade-off and conflicts between conservation vs. development and the difficulty in integrating political regulations with conservation projects conducted by different stakeholders (Dirzo and Loreau 2005, Tabarelli et al. 2005). Implementing biodiversity conservation with the considerations of socio-economic costs, needs for sustainable development, and political aids remains the top priority.

Ferrier (2002) proposed two strategies to use biodiversity data more effectively. These strategies entail a close integration of biological and environmental data via predictive modeling of biodiversity properties and the use of remote sensing maps of biodiversity surrogates and land heterogeneity information for conservation planning. For example, Saatchi et al. (2008) found that combining climate-based and remote sensing-based species distribution models provide complementary results of Amazonian tree distribution patterns. Remote sensing can expand the array of information used in conservation and management (Wiens et al. 2009). I hereby suggest embracing the framework of systematic conservation planning for maximizing the efficiency of integrating remote sensing, biodiversity conservation, and consideration of sustainable development at the landscape and regional scales.

Systematic conservation planning

Building upon the understanding of biodiversity patterns, conservation biogeography aims to apply the understanding to practical conservation issues. Human-nature interactions plays a key role in conservation biogeography with an emphasis on biogeographic patterns, natural resource management, conservation of biodiversity, environmental degradation and planning, and sustainable development (Young et al.

2003, Quattrochi et al. 2003, Bassett and Zimmerer 2003). Geographers seek to develop strategies for minimizing conflicts between natural resource utilization and biodiversity conservation as well as for reducing the impact of deforestation and habitat fragmentation (Bassett and Zimmerer 2003). Current geographic studies should provide insights to link traditional interest in human-environment interactions and the emergent needs for conservation planning. My dissertation research uses climatic, topographic, hydrological, remote sensing, and environmental data to identify conservation prioritization areas.

In the 1980s the central goal of conservation began to shift as conservationists sought to use detailed biogeographic distribution data in designing zonation maps (Margules et al. 1988). The demand for integrating socio-economic criteria and the use of computer algorithms to process large datasets had also emerged by the 1990s (Sarkar et al. 2006). Margules and Pressey (2000) formulated the framework of systematic conservation planning. The primary aim is to maintain representation and persistence of biodiversity. Differing from traditional ad hoc improvised conservation planning, systematic conservation planning selects biodiversity zonation maps. It formulates management plans by using step-wise protocols to identify conservation priority areas and to separate them from potential threats (Pressey et al. 1996, Margules et al. 2002). The key concept that formulates this framework is complementarity, a measure of how much an area within a planning region contributes to fully complementing biodiversity features and conservation goals (Margules and Sarkar 2007). Thus, conservation planning tools must identify either sets of complementarity areas for achieving quantitative targets or the complementarity contribution of individual areas (Sarkar et al. 2006).

Systematic conservation planning takes complementarity and maximizing spatial connectivity among selected conservation prioritization areas within the network as the most important concepts based upon the primary goals of maintaining biodiversity

representation and persistence (Nicholls and Margules 1993). Hence, it has obviously moved forward beyond the traditional island biogeography theory in order to create a more integrative and complex agenda for biodiversity conservation (Margules et al. 1988, Margules and Pressy 2000).

The original systematic conservation planning framework consisted of six stages: 1) compile and refine biodiversity and socio-economic data, 2) identify conservation goals, 3) review existing conservation areas, 4) prioritize additional conservation areas, 5) implement conservation, and 6) periodically reassess the zonation map (Margules and Pressey 2000). After stakeholders, biodiversity representation and persistence, and conservation feasibility are taken into account, a newer framework has been expanded with these additional stages: 1) identify stakeholders, 2) identify biodiversity surrogates, 3) assess the persistence of biodiversity surrogates in newly prioritized areas, 4) refine zonation maps, and 5) use multi-criteria analysis to examine project feasibility (Margules and Sarkar 2007). The most updated protocol for systematic conservation planning added specific components of 1) choose and delimit planning area, 2) treat data and construct models, and 3) set explicit goals and targets (Sarkar and Illoldi-Rangel 2010).

Conservation planning should take place at the earliest stage of development to maximize biodiversity features in a conservation network (Margules et al. 1988). Because biological entities consist of either a spatial (ecological) hierarchy from molecules to biosphere or a taxonomic one from alleles to kingdoms, biodiversity can refer to diversity at levels of genes, species, and ecosystems (Sarkar 1998, Margules and Sarkar 2007). The definition of biodiversity does not need to be arbitrary because all levels of diversity contain a great extent of variety and heterogeneity (Margules and Sarkar 2007). As Austin and Margules (1986) pointed out, biodiversity features must correspond to what are quantifiable and assessable such as species or taxa presence and habitat types. The

ultimate goal of defining suitable units within the biodiversity hierarchy should focus on matching conservation targets and efforts with each level of the hierarchy.

Niche modeling is often used to fill in species distribution for areas that lack adequate species surveys in remote regions. Niche models can derive from ecological knowledge-based models (Wright et al. 2006), statistical association models (Etienne and Olff 2005), or machine-learning methods using algorithms based on past success to predict future associations between species presence and environmental variables (Drake et al. 2006). Alternatively, high-resolution remote sensing data may provide species information and therefore, serve as sources for species occurrence data and environmental variables (Sarkar and Illoldi-Rangel 2010).

More specifically, conservation prioritization requires identifying biodiversity surrogates and selecting areas to achieve target surrogate representation (Margules and Sarkar 2007). True surrogates can be detailed habitat and vegetation classes derived from classified remote sensing images, whereas estimator surrogates can be 1) environmental surrogates using environmental, climatic, topographic, and hydrological data and 2) biological surrogates of species whose potential habitats are predicted using niche modeling based on species presence in remote sensing images (Phillips et al. 2006). Subsequent habitat-based viability analysis or risk analysis has to take place in order to examine species persistence, and habitat size, shape and spatial connectivity in the selected conservation prioritization zones. Finally, a multi-criteria analysis that integrates the best solutions for a zonation map with other social, political, economic, and cultural criteria will assist in determining how conservation projects should be implemented (Sarakinos et al. 2001, Fuller and Sarkar, 2006).

Conservation planning should examine the extent to which biodiversity varies spatially and the hierarchical heterogeneity in environmental factors and vegetation types

within which surrogates are used (Faith et al. 2001a, Sarkar and Margules 2002). Selecting biodiversity surrogates according to environmental connectivity and heterogeneity will maximize the usefulness of surrogates (Lindenmayer et al. 2000, Ferrier 2002). In addition, remote sensing data can become part of the surrogates for the ultimate goal of capturing environmental gradients (Venevsky and Venevskaia 2005, Rouget et al. 2006). Determining targets of surrogate representation within a zonation map must take place based on the variation in species and the environment, shape and connectivity of the landscape, and potential socio-political influences (Faith et al. 2001b). Place prioritization that ranks areas in terms of their contribution to target representation should follow (Brownlee et al. 2005). The area minimization approach finds minimum sets of sites whereas the representation maximization approach looks for sites that maximize the number of surrogates that meet the targets. The most important prioritization rule employs complementarity that measures what a new site contributes to the biodiversity representation among existing sites for complementing beta diversity (Williams et al. 1996). Subsequently, habitat-based viability analysis or risk analysis can contribute to examining species persistence, and habitat size, shape and spatial connectivity in order to assess selected sites (Sarakinos et al. 2001, Fuller et al. 2006).

Most previous studies that identified conservation prioritization zones focused on selecting either environmental or biological surrogates (Cowling et al. 2004, Ferrier et al. 2004). Moreover, these studies mostly relied on plot-based, time consuming, and labor intensive inventory data. Consequently, they were unable to conduct conservation projects in remote unsampled areas. Due to the limitation in data availability, my dissertation research combines remote sensing and biophysical environment data to create zonation maps as an exercise to select areas within various landscape features based on different criteria specified by the researcher.

STUDY OBJECTIVES

This dissertation, centered by the foundation of conservation biogeography, first aims to examine a few well-discussed mechanisms that influence alpha and beta diversity patterns of the Amazonian trees. Multiple analyses are carried out to elucidate whether or not alpha and beta diversity patterns are associated with environmental factors, neutrality, or dispersal limitation. Niche partitioning in association with interspecific competition cannot be examined due to the lack of temporal data. I also utilize remotely sensed data and techniques to map features of forest canopies that are essential elements of alpha and beta diversity. At a coarse scale, I use remote sensing tools to classify the landscape that harbors heterogeneous biodiversity components. The remote sensing-based information is used for creating zonation maps that show site selections based on various preferences and spatial criteria. The ultimate goal is to provide baseline information for applied conservation biogeography in the future, under the framework of systematic conservation planning.

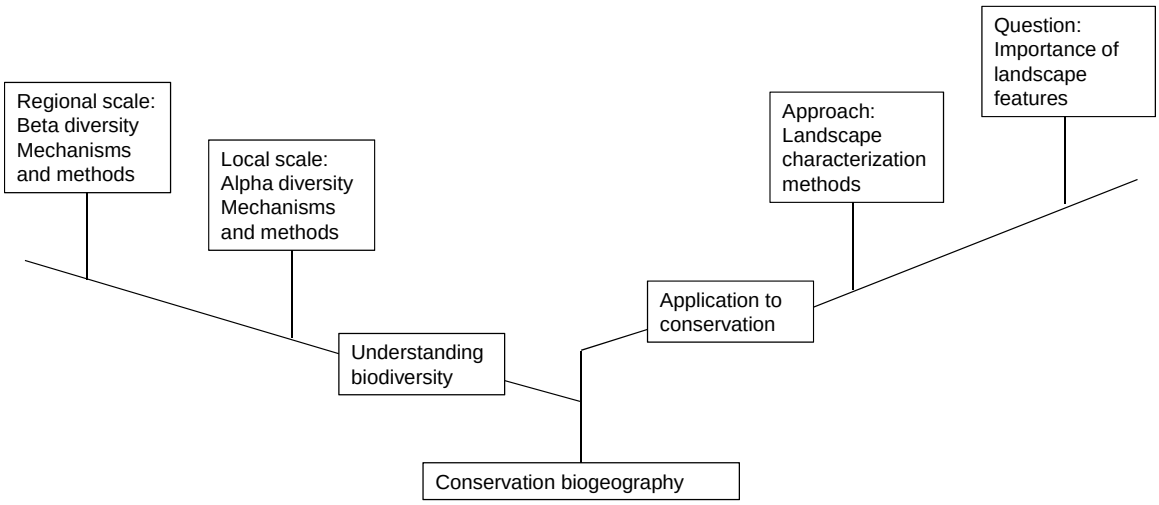
Specific objectives of my dissertation research are to 1) examine the degree of similarity between spatial heterogeneity of tree diversity patterns measured at a local scale and the spatial heterogeneity detectable at a regional scale and 2) take a remote sensing-based approach in data acquisition and analysis to provide landscape zonation maps within the Achuar, Shiwiar, and Zapara indigenous territories in the Ecuadorian Amazon. Fine resolution remote sensing images are used for examining tree density and distribution at the local scale. Meanwhile, I characterize habitat types based on classifications from coarse-resolution remote sensing images at the regional scale.

SPECIFIC QUESTIONS AND HYPOTHESES

By having conservation biogeography as the theoretical basis, the conceptual framework of my dissertation entails elements to understand biodiversity patterns and to

apply the understandings towards conservation (Figure 1.1). I aim to employ a two-scale (local and regional) approach to examine mechanisms that contribute to alpha and beta diversity, as well as examining remote sensing-based methods towards applications of biodiversity studies on conservation. By examining remote sensing methods that characterize landscape features which harbor biodiversity components and evaluate the importance of landscape features, this dissertation links theories and potential real-world science of conservation biogeography together.

Figure 1.1. The conceptual framework and methodology of my dissertation.



To examine the mechanisms that influence alpha diversity and to elucidate spatial distribution patterns of trees, I ask:

Q1. For three southeastern Ecuadorian one-ha plots, to what extent is the within- and between-plot variation in tree species diversity and distribution affected by the local biophysical environment? Do size class and height of trees show random or clustered distributions?

H1. The within- and between-plot spatial heterogeneity in tree distribution (within a plot), and species diversity (within- and between-plot) is not randomly distributed. Species distribute along a gradient of heterogeneous canopy opening, soil properties, or topography. Habitat associations or spatial relationships with other individuals are observed.

At the regional scale, I aim to examine what contributes to beta diversity patterns by asking:

Q2. Do beta diversity patterns and distribution of trees among plots in southeastern Ecuador, northeastern Ecuador, and northern Peru vary along a geographic gradient? What contributes to the floristic variation at the regional scale?

H2. The differences in tree species diversity and distribution between southeastern Ecuador and other plots increase with their geographic distances. The bioclimatic or topographic differences among the regions where tree plots are located account for the beta diversity patterns and between-plot differences. Patterns of species rarity and dominance differ among the three regions.

To examine the extent to which fine-scale remote sensing data inform about canopy features that characterize forest structure and community, I ask:

Q3. Do canopy shadows extracted from aerial photographs successfully represent real canopy shadows that contain important forest canopy features? Do common canopy palm species that are detectable from aerial photographs provide density and distribution information complementary to ground inventories in the Amazon?

H3. Canopy shadows that are extracted from aerial photographs using object-based classification are highly representative of real canopy shadows. Palm density and distribution based on aerial photographs can contribute to examining the spatial dimensions of certain palm species in the Achuar, Shwiar, and Zapara territories.

To characterize landscape features and create landscape zonation maps, I ask:

Q4. What is the best approach for a zonation map design that embodies spatial criteria and preferences among landscape features by using remote sensing and GIS information?

Goal: To provide maps of landscape zonation that categorizes particular objectives for future conservation work in the Achuar, Shwiar, and Zapara territories. The production of zonation maps takes place using analysis that embodies remote sensing data of habitat classification and topography, as well as GIS data of local land use, soil, and hydrology.

In the following chapters I first introduce the study regions in southeastern Ecuador and in western Amazon. I then describe data acquisition and analysis methods for each of the abovementioned questions, hypotheses, and goals. Results and discussions for each specific question and hypothesis/goal are organized into individual chapters, followed by a conclusion chapter to summarize major findings and contributions of this dissertation towards enriching the discipline of conservation biogeography.

Chapter 2: Study area

THE ECUADORIAN AMAZON

The study area in southeastern Ecuador corresponds to several indigenous territories in the Ecuadorian Amazon. The three 1-ha tree inventory plots in southeastern Ecuador were located in a 15,185 km^2 study area (1°30'S, 76°30'W), at the western margin of the Amazon and 100 km from the Andean foothills. This area belongs to the Morona Santiago and Pastaza provinces of Ecuador. It comprises indigenous territories of the Achuar, Shiwiar, Zapara, and part of the Kichwa (Figure 2.1). The estimated population of the Achuar is 6,000 (NAE 2007, http://www.nacionalidadachuarecuador.org), of the Shiwiar is 1,200 (NASHIE 2007, http://www.shiwiar-ecuador.org), and of the Zapara is 200 (INEC 2003, http://www.inec.gov.ec). Although the dissertation's study area covers the Zapara and part of the Kichwa territories, the fine-scale tree inventory and aerial photograph studies focused on the communities in Achuar and Shiwiar territories (Illustration 2.1A, 2.1B). Both Achuar and Shiwiar belong to the Jivaro indigenous family, one of the largest indigenous groups in the Amazon (Descola 1987).

Illustration 2.1. Residential areas in the communities of Yutsuntsa (A) in Achuar and Juyuintsa (B) in Shiwiar territories.

A.

B.

La Nacionalidad Achuar de Ecuador (NAE), recognized by the Development Counsel of the Indigenous Nationalities and Communities of Ecuador (CODENPE) in 2005, represents the Achuar in Ecuador. NAE's territory extends between the parallels 1°45'S and 2° 50'S, bordering with Peru, and 77° 38'W and 76° 20'W, which comprises an area of 6,814 km^2. NAE consists of nine grassroots associations, 68 communities, and about 6,000 people (NAE 2007) (Illustration 2.2). The estimated annual population growth rate is approximately 5%. The estimated population density is about 0.86/km^2 (Lopez 2008) (Figure 2.2). The Achuar occupies a region drained by large fluvial systems. NAE's territory is characterized by gentle depressions corresponding to old fluvial terraces of the Pastaza River. These depressions are permanently inundated and covered almost uniformly by patches of *Mauritia flexuosa* palms (Lopez 2008).

Figure 2.1: Map of the study area showing the Morona Santiago and Pastaza provinces, the indigenous territory names in bold, and major rivers. Yasuní National Park is indicated in red (GIS data sources: NAE and NASHIE 2006, provided by R. Sierra and M. Peralvo).

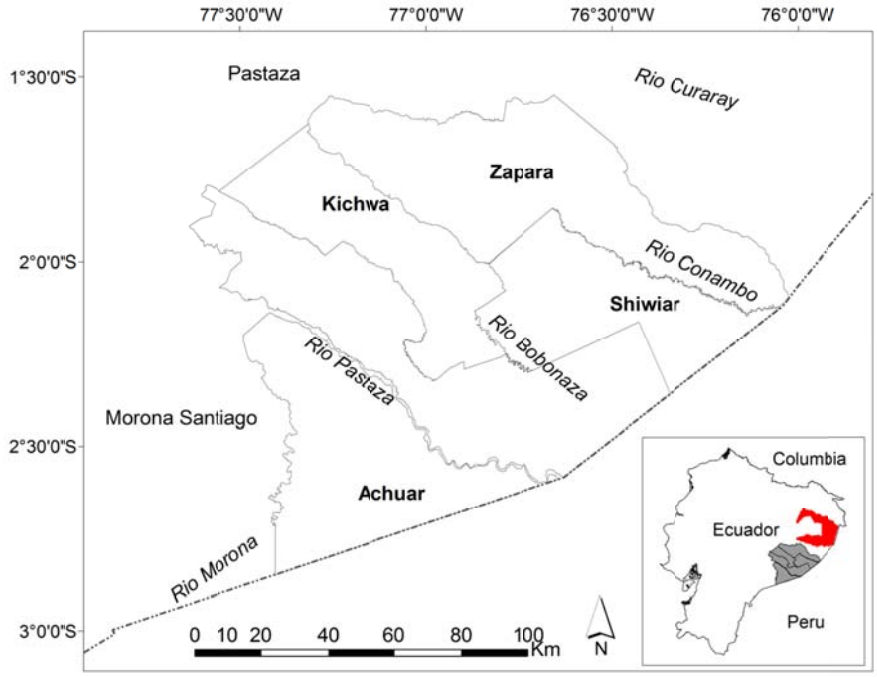
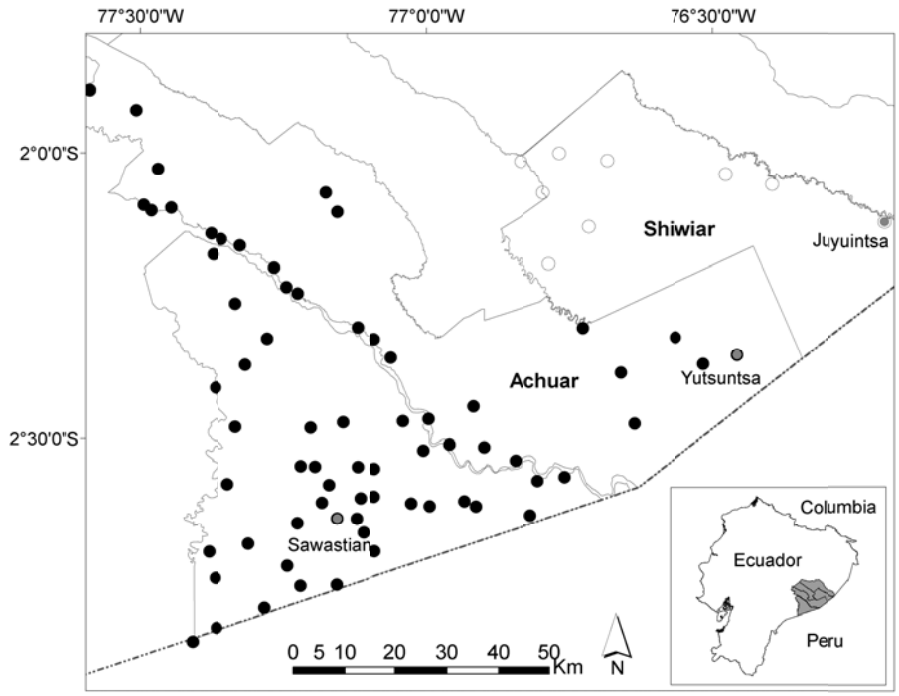


Illustration 2.2. People in the Sawastian community in Achuar.

Figure 2.2. Distributions of the Achuar (in black) and Shiwiar (in white) communities. The tree inventory plots are located in the communities shown in grey. (GIS data source: NAE and NASHIE 2006, provided by S. Lopez)



La Nacionalidad Shiwiar del Ecuador (NASHIE) represents nine communities and about 1,200 Shiwiar people (NASHIE, 2006) (Figure 2.2). The Shiwiar territory extends between 1°50'S and 2°36'S, and 76°52'Wand 76°2'W with a total area about 2,211 km2. The annual population growth rate is approximately 5.6%. The population density is 0.54/km^2 (Illustration 2.3). The Bufeo and Kurintza communities contain more than half of the total population (Lopez 2008).

Illustration 2.3. People in the Juyuintsa community in Shiwiar.

Climate

Climate data of the study area came from the WorldClim dataset, (http://www.worldclim.org/), a set of climate data layers with a spatial resolution of approximately 1 km. Variables in the data layers include monthly precipitation and temperature, as well as 19 derived bioclimatic variables. These variables were derived from spatial interpolation of climate data from 1950-2000 (Hijmans et al. 2005). The study area contains an annual mean temperature that ranges between 23.2-25.7 °C with a mean annual range of 11.4 °C between the maximum of the warmest and the minimum of the coldest months. The average of maximum temperature of the warmest month is 30.9 °C whereas the average of minimum temperature of the coolest month is 19.5 °C.

The study area for the three 1-ha plots has an annual precipitation that ranges between 2558-3715 mm, with a mean rainfall of 200.7 mm in the driest month and a

mean of 323.7 mm in the wettest month. There is no distinctive dry season in the area, but seasonal variation is stronger within precipitation data than with temperature data. The average monthly precipitation is the lowest in December, January, and February. Overall, rainfall is the highest from March through July. In contrast, mean monthly temperature of the study area shows little variation (Figure 2.3). August is a transitional month that either prolongs the rainy season or inaugurates an early drier season (Descola, 1994). The area with the highest annual mean temperature is also the area with the lowest annual precipitation; it occurs at the southern tip of the study area. Annual mean temperature decreases and annual precipitation increase along a gradient northward to the northwestern corner of the study area (Figure 2.4).

The Andes plays an important role in modifying the atmospheric circulation of low inter-tropical pressure by maintaining dense masses of humid air. The increase in temperature and the decrease in precipitation progress inversely along the altitude (Lopez 2008). As the elevation in Achuar decreases towards the east from 500 m to less than 200 m, the average annual temperature increases from 20.3 °C to 23.9 °C (Lopez 2008).

Figure 2.3. Mean monthly temperature (in scattered line) and precipitation (in bars) of the study area (data obtained from WorldClim).

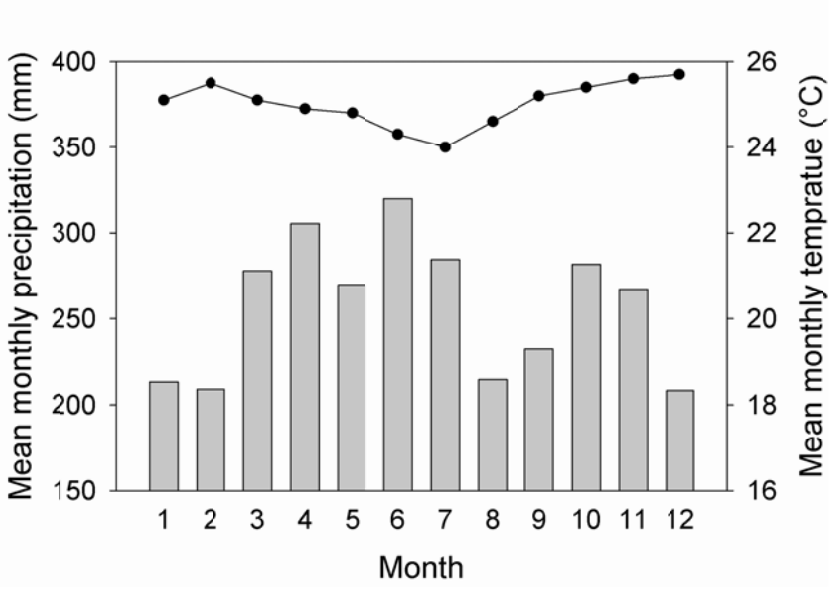
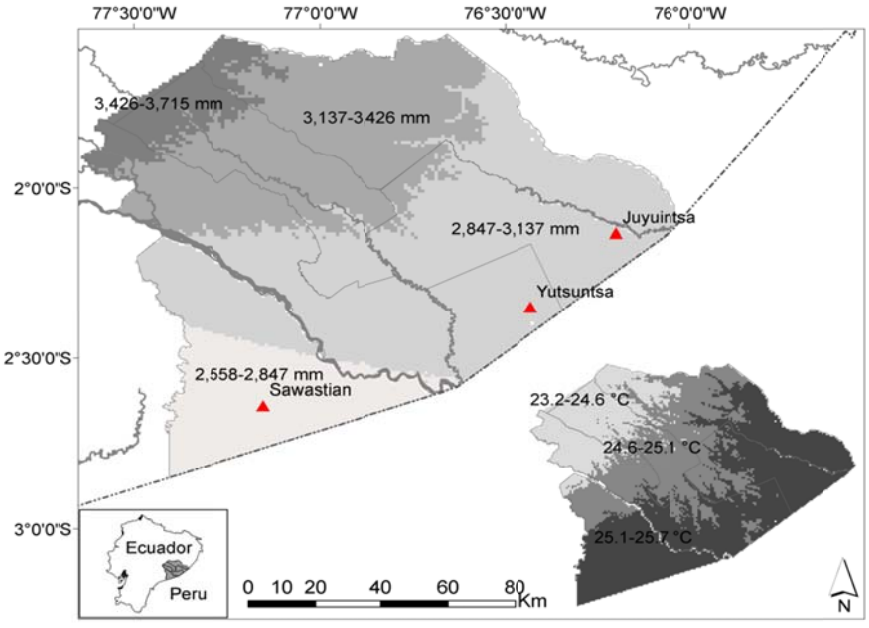


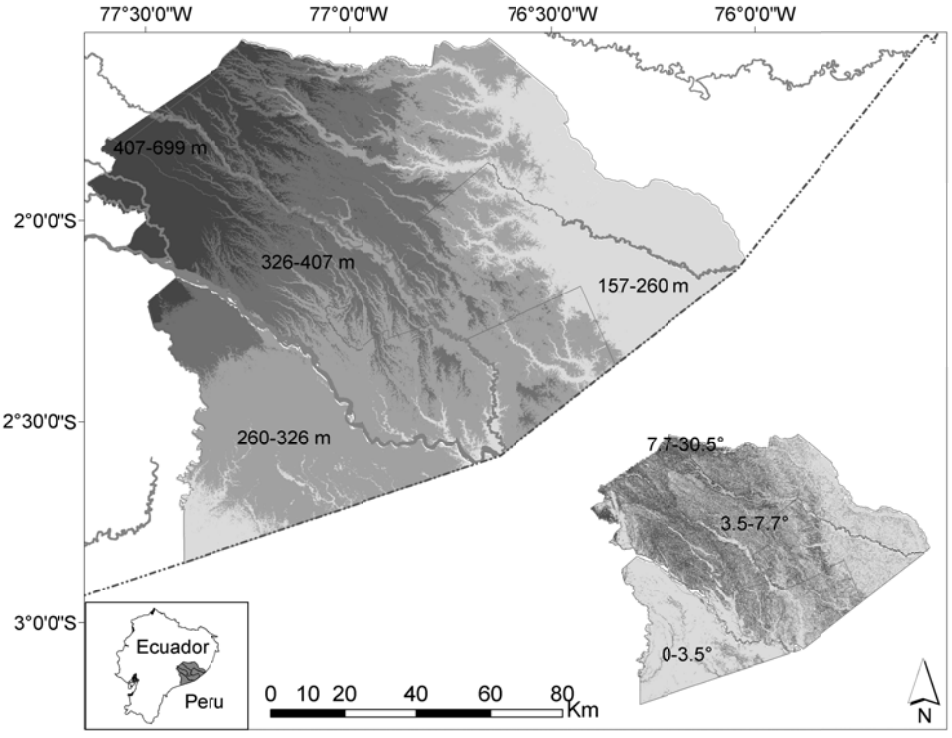
Figure 2.4. Annual mean temperature (small map) and annual precipitation (large map) of the study area, including the locations of three 1-ha tree inventory plots (in red) (data obtained from WorldClim).



Topography

A digital elevation model (DEM) derived from NASA's Shuttle Radar Topography Mission (SRTM) was acquired from United States Geological Survey (USGS) at a 90-m resolution. Elevation of the study area ranges between 157-699 m, with an average of 314 m (Figure 2.5). The lowest elevation occurs in most of the areas south of Rio Pastaza and in areas just south and north of Rio Conambo. The highest elevation can be found on the western side of the study area. Likewise, the gentlest slopes occur in the lowland terrain (Figure 2.5). There is no dominant slope direction. Curvature of elevation varies greatly, indicating a great topographic heterogeneity of the study area.

Figure 2.5. Elevation (large map) and slope (small map) of the study area (data obtained from SRTM). See Figure 2.4 for the locations of three 1-ha tree inventory plots.



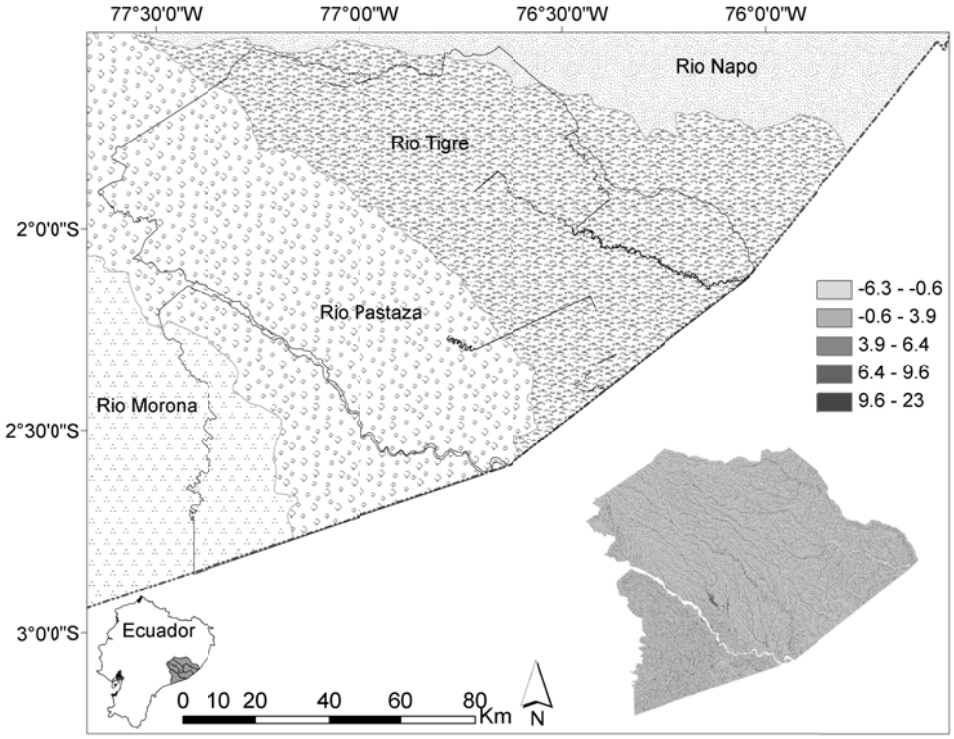
Hydrology

Major rivers that run through the study area include Rio Pintoyacu, Rio Conambo, Rio Bobonaza, and Rio Pastaza from north to south. The entire study area belongs to the large Amazon drainage basin, an area of 5,912,929 km^2. From south to north the study area comprises basins of Rio Morona, Rio Pastaza, Rio Tigre, and Rio Napo in respective areas of 1126, 7255, 6702, and 101 km^2 (Figure 2.6). Elevation of the Morona and Pastaza basins ranges between 240-621 m with an average of 339 m. Elevation of the Tigre basin is 198-396 m at the mean of 264 m. Elevation of the Napo basin lies between 246-285 m with an average of 266 m. Sub-basins in this area from south to north include Rio Morona, Rio Huasaga, Rio Copotaza, Rio Chundayacu, Rio Ishpingo, Rio Bobonaza, Rio Corrientes, Rio Conambo, Rio Pintoyacu, and Rio Curaray (Illustration 2.4).

Illustration 2.4. A river that runs through the Juyuintsa community in Shiwiar.

Compound Topographic Index (CTI) is a function of the upstream contributing area and the slope of the landscape (USGS 1998). CTI reflects the tendency of water to accumulate in a catchment and the tendency to move down slope due to gravitational forces. CTI in the study area shows a wide range, indicating the heterogeneity of the hydrological landscape in relation to the topography (Figure 2.6).

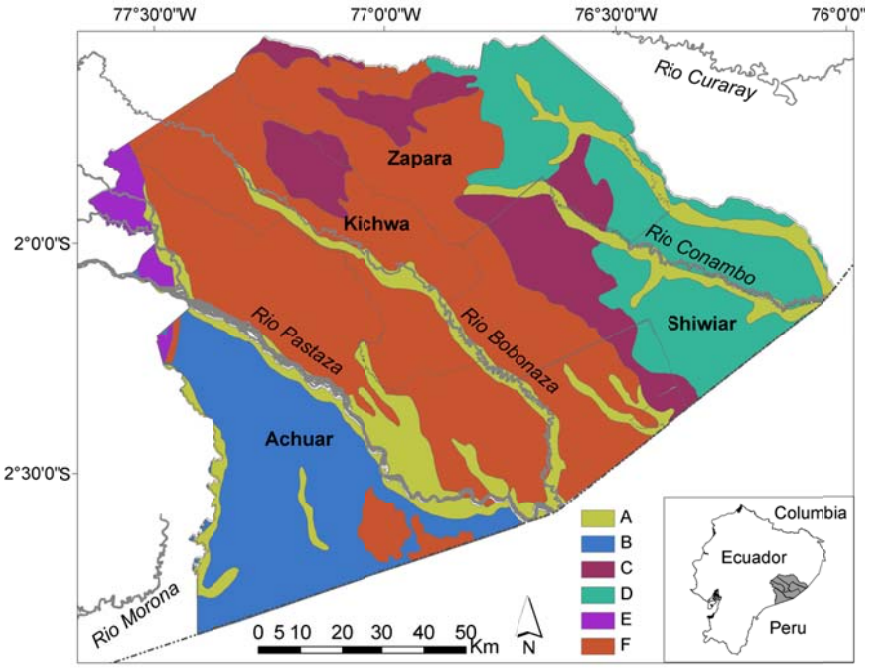
Figure 2.6. Major drainage basins (Rio Morona, Rio Pastaza, Rio Tigre, and Rio Napo) shown in different patterns (large map) and CTI (small map) of the study area (drainage data source: Instituto Geografico Militar (IGM) in Quito, Ecuador (various maps) and provided by R. Sierra, CTI calculated by Y.H. Wang). See Figure 2.4 for the locations of three 1-ha tree inventory plots.



Geology

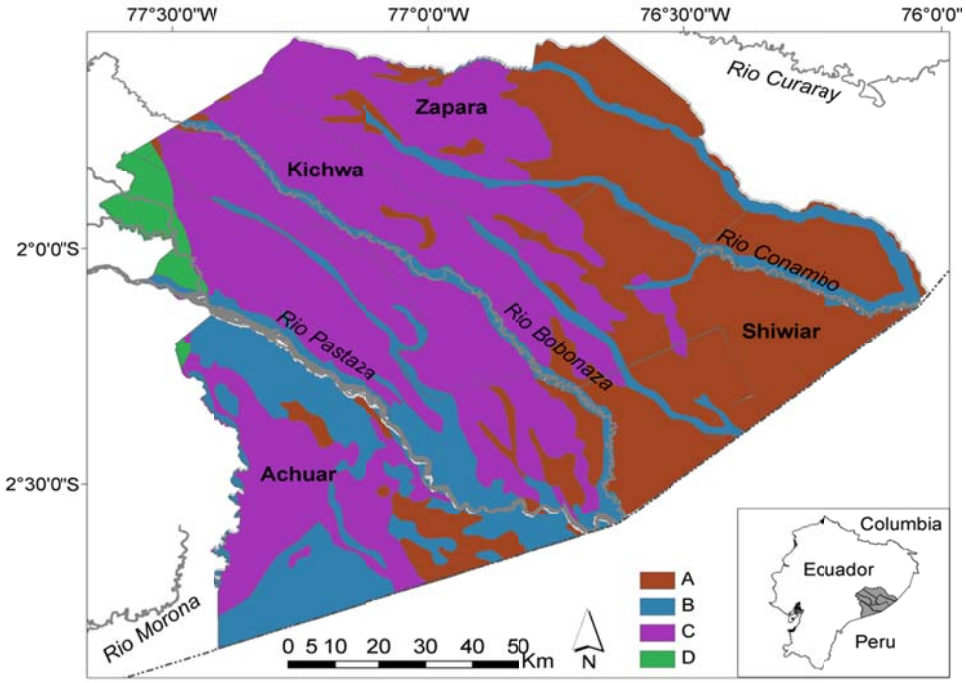
A coarse-scale geology map shows six geological layers in the study area: the most recent Quaternary alluvial deposits with clay and sand (A), Quaternary Mera terrace (50-200 m) with a sand and lutite conglomerate (B), Quaternary-Pliocene Mesa (10-400 m) layer with sandstone conglomerate and volcaniclastic sediments (C), Miocene Curaray (200-700 m) with clay, soft calcareous lutite rock, and gypsum (D), Miocene Araujo (500-1000 m) with clay, sandstone, and lignite (E), and the oldest layer of Pliocene-Miocene Chambira (1000-1500 m) with sandstone, lutite, and soft calcareous rock (F) (Figure 2.7).

Figure 2.7. Geology layers of the study area. See the text for figure legend (GIS data source: Dirección Nacional de Recursos Naturales (DINAREN) in Quito, Ecuador (1983-1986 maps) and provided by R. Sierra). See Figure 2.4 for the locations of three 1-ha tree inventory plots.



From a geomorphology perspective, the study area contains 1) peri-Andean slopes with sandstone and clay conglomerate with cover of ferralitic soil and pseudo-ferralitic red soil (A), 2) half alluvium (B), 3) piedmont (C), and 4) sub-Andean buttress derived from sedimentary relief with clay and sandstone that is partially the exhumation of piedmont formation (D) (Figure 2.8). A national map of seismic risk indicates that the area may experience three types of risk: 1) low subduction seismicity, 2) inverse front sub-Andean fault and inverse subduction fault, and 3) high seismicity.

Figure 2.8. Geomorphology layers of the study area. See the text for figure legend (GIS data source: Dirección Nacional de Recursos Naturales (DINAREN) in Quito, Ecuador (1983-1986 maps) and provided by R. Sierra). See Figure 2.4 for the locations of three 1-ha tree inventory plots.



Soil

A coarse soil classification map shows that soil types in the study area include Entisol Tropofluvent, Entisol Troporthent, Histosol Tropofibrist, Inceptisol Hydrandept, Inceptisol Tropaquept, and Inceptisol Dystropept (Figure 2.9). A more detailed classification, however, shows 17 soil types in the Achuar, Shiwiar, and Zapara territories (Figure 2.10, 2.11).

In particular, the Achuar territory occupies low terraces in the alluvial basins. These terraces present alluvial volcanic soil (Fluvent Tropaquepts) or dark soil with a high potential fertility. These areas correspond to soil type K (Figure 2.10, 2.11). The physical and chemical characteristics make type K the best soil in the entire Achuar territory because the pH ranges from 5.5-6.5, the interchangeable aluminum amount is low, and the organic matter content is high (Descola 1987). The Achuar territory also contains high terraces that consist of ferralitic red soil (Typic or Oxic Dystropepts) with high aluminum content or of a mixture of red and sandy soil produced by the erosion of hills. These areas belong to soil types F and H in inter-fluvial habitats (Figure 2.10, 2.11) (Lopez 2008). The Achuar territory also contains recent alluvial terraces and swampy alluvial floodplains with large inundated depressions. The soil type is Tropofibrist and is rich in organic matter, which supports dominant palm vegetation (Lopez 2008).

The Shiwiar territory contains high inter-fluvial alluvial terraces. The soil is Typic or Oxic Dystropepts, generally red sandy soil with low fertility and with high aluminum content (Descola, 1994). Some terraces have Vitrandepts, Dystrandepts, and Aquic Dystropepts soils (Figure 2.10) (Lopez 2008).

Figure 2.9. Coarse soil map of the study area. Ent_Flu = Entisol Fluvent, Ent_Ort = Entisol Orthent, His_Fib = Histosol Fibrist, Inc_And = Inceptisol Andept, Inc_Aqu = Inceptisol Aquept and Inc_Tro = Inceptosol Tropept (GIS data source: Dirección Nacional de Recursos Naturales (DINAREN) in Quito, Ecuador (1983-1986 maps) and provided by R. Sierra). See Figure 2.4 for the locations of three 1-ha tree inventory plots.

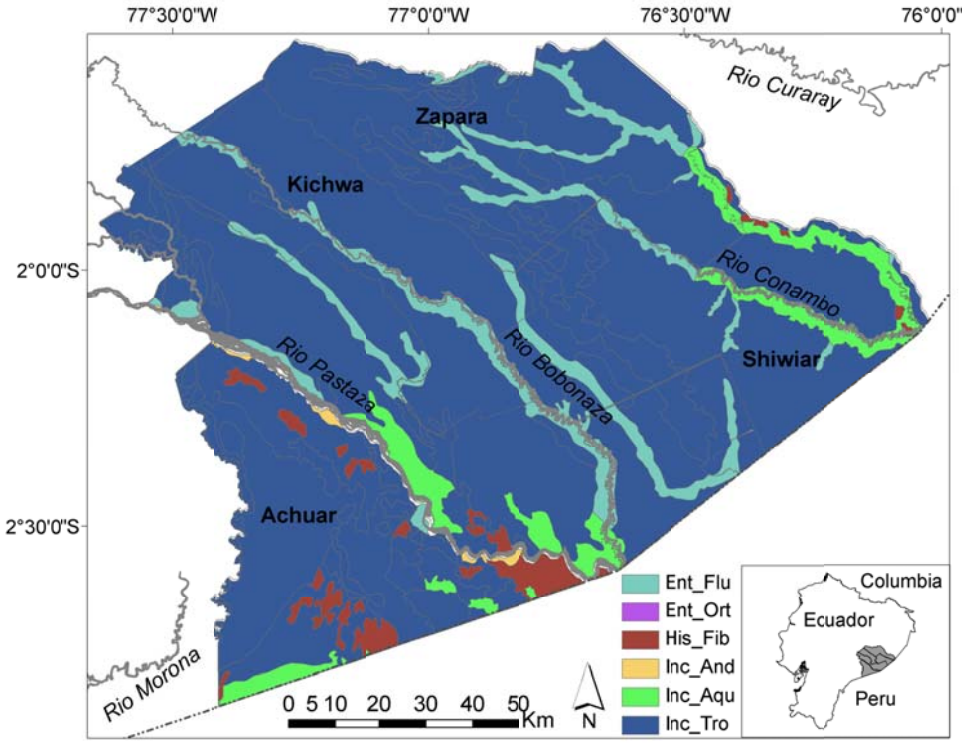


Figure 2.10. Detailed soil map of the Achuar, Shiwiar, and Zapara territories. See Figure 2.11 for figure legend (GIS data source: Custode 1983 and refined by Lopez 2008). See Figure 2.4 for the locations of three 1-ha tree inventory plots.

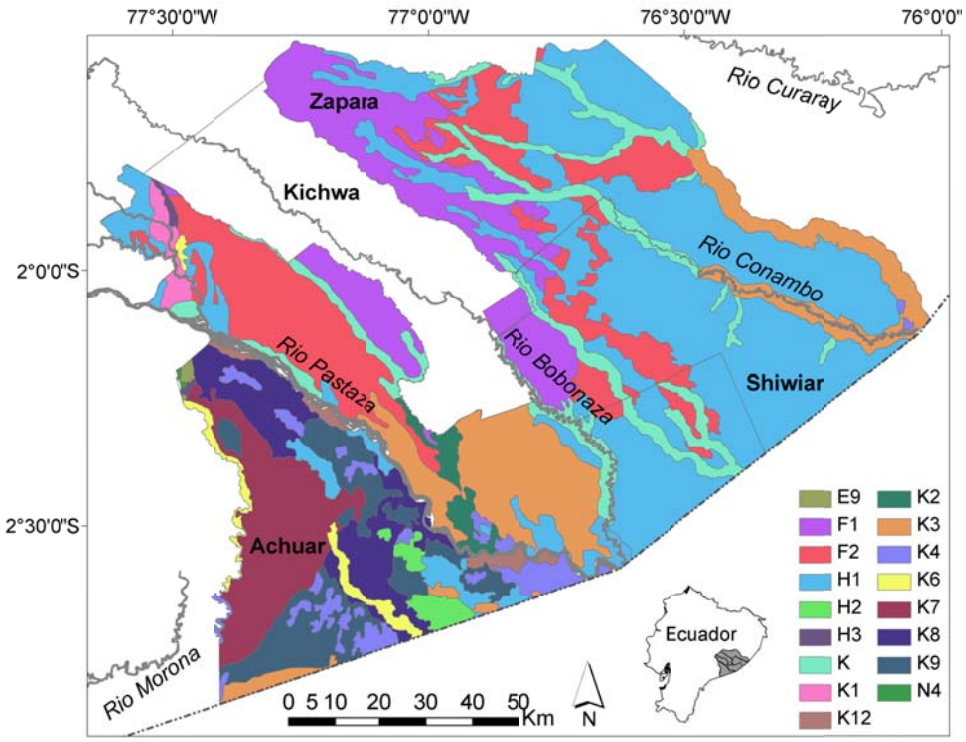


Figure 2.11. Soil identification codes and their respective soil types, geomorphologic features, and characteristics in the Achuar, Shiwiar, and Zapara territories (From Table 4.2 in Lopez 2008).

SOIL ID	*SOIL TYPE*	*GEOMORPHOLOGIC FEATURES*	*CHARACTERISTIC*
N4	Typic DYSTROPEPTS (red soils)	Foothills topography and irregular hills	Less deep lime and clay red soils; low fertility and high aluminum content
E9	Oxic DYSTROPEPTS HAPLORTHOX (red and brown soils)	Old alluvial fans and dissected floodplains. Terraces and cliffs.	Deep clayey soils, with low fertility, and very high aluminum content
F1	Oxic DYSTROPEPTS (red and brown soils) and HAPLORTHOX	Deeply dissected mesas	Very deep clayey soils with very low fertility (brown soils), low fertility (red soils), and toxic aluminum
F2	Oxic or Typic DYSTROPEPTS (red soils)	Irregular topography derived from mesas.	Very deep clayey soils
H1	Oxic or Typic DYSTROPEPTS (red soils)	Hills	Shallow clayey and loamy soils, with low fertility and toxic aluminum
H2	Oxic or Typic DYSTROPEPTS (red soils) and TROPAQUEPTS	Hills surrounded by swamps	Shallow red clayey and loamy soils, with low fertility and toxic aluminum. Variable fertility with a superficial phreatic layer
H3	ORTHENTS and Oxic DYSTROPEPTS	Chevrons	Sandy soils, with low or no fertility
K1	DYSTROPEPTS EUTROPEPTS	Medium level alluvial terraces	Soils with variable fertility, generally fertile
K2	Aquic DYSTROPEPTS TROPAQUEPTS	Low alluvial terraces	Soils with high water content or "gley"
K3	TROPAQUEPTS	Floodplains and depressions	Complex of soils with variable fertility and superficial phreatic layer
K4	Hydric TROFIBRISTS	Depressions and oxbow lakes	Poor drainage, multiple limitations with organic matter
K6	Aquic DYSTROPEPTS and Fluventic TROPAQUEPTS	Terraces of the Cangaime, Huasaga, and Macuma Rivers	Low fertility, with toxic aluminum; high fertility and high phreatic layer

SOIL ID	SOIL TYPE	GEOMORPHOLOGIC FEATURES	CHARACTERISTIC
K7	Oxic HAPLORTHOX Typic and Aquic DYSTROPEPTS (pardos) TROPAQUEPTS	Flat and slightly hilly floodplains drained by creeks	Soils with variable characteristics depending on their thickness; some are deep and clayey, with low fertility and toxic aluminum; others are thinner and siltier with medium fertility and limited drainage
K8	Oxic HAPLORTHOX Typic and Aquic DYSTROPEPTS (pardos) TROPAQUEPTS	Flat floodplains with imperfect drainage	Soils with variable characteristics depending on their thickness; some are deep and clayey, with low fertility and toxic aluminum; others are thinner and siltier with medium fertility and limited drainage
K9	K4 and K6 COMPLEX	Mixed features of K4 and K6	See K4 and K6
K12	Aquic HYDRANDEPTS (upstream)	Terraces of the Pastaza and Upano Rivers	Soils generally deep and loose with imperfect drainage and risk of flooding
K	Complex of K units	Complex of terraces with different levels	Characterisitcs of K soils units.

Vegetation

The study area belongs to the "tropical humid forest" category in the Holdrige life zone system (Holdridge et al. 1971). An early vegetation classification divides the study area into lowland white-water floodable forests, Amazonian foothill evergreen forests, Amazonian lowland evergreen forests, lowland palm and black-water forests, and intervened zones (Sierra 1999) (Figure 2.12). A recent vegetation and land cover classification produced by Lopez (2008) further divides the Achuar and Shiwiar territories into nine classes: human land use, lowland evergreen forests on flat terrain, lowland evergreen forests in floodable white water, lowland evergreen forests on hilly

terrain, palm swamps, secondary vegetation, shrub and grass vegetation, upper lowland evergreen forests on hilly terrain, and water (Figure 2.13).

Figure 2.12. Coarse vegetation map of the study area (Sierra 1999). See Figure 2.4 for the locations of three 1-ha tree inventory plots.

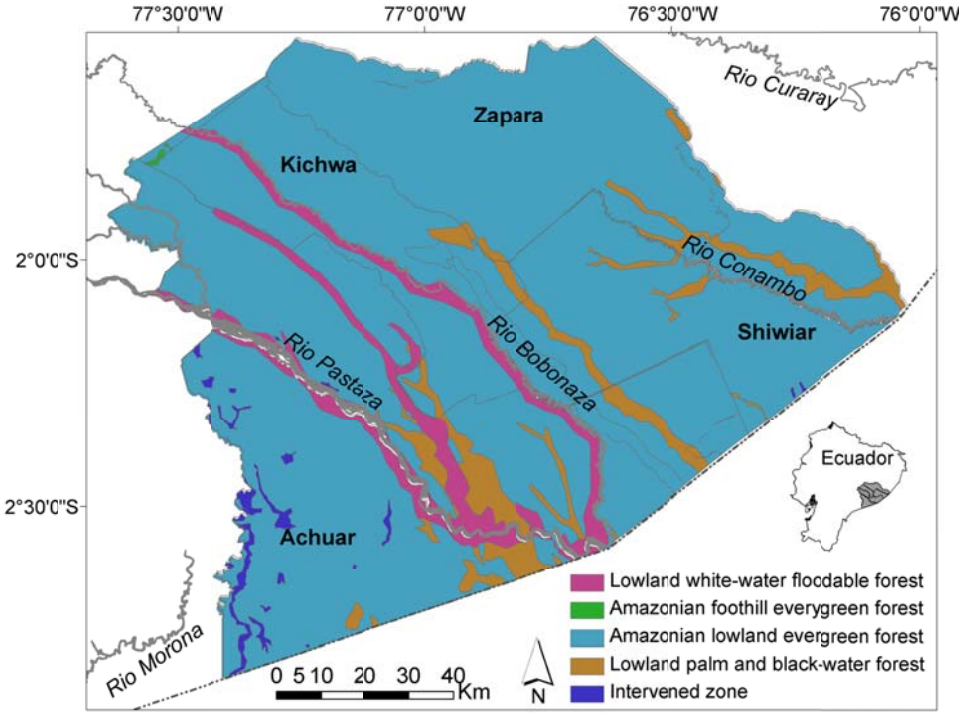
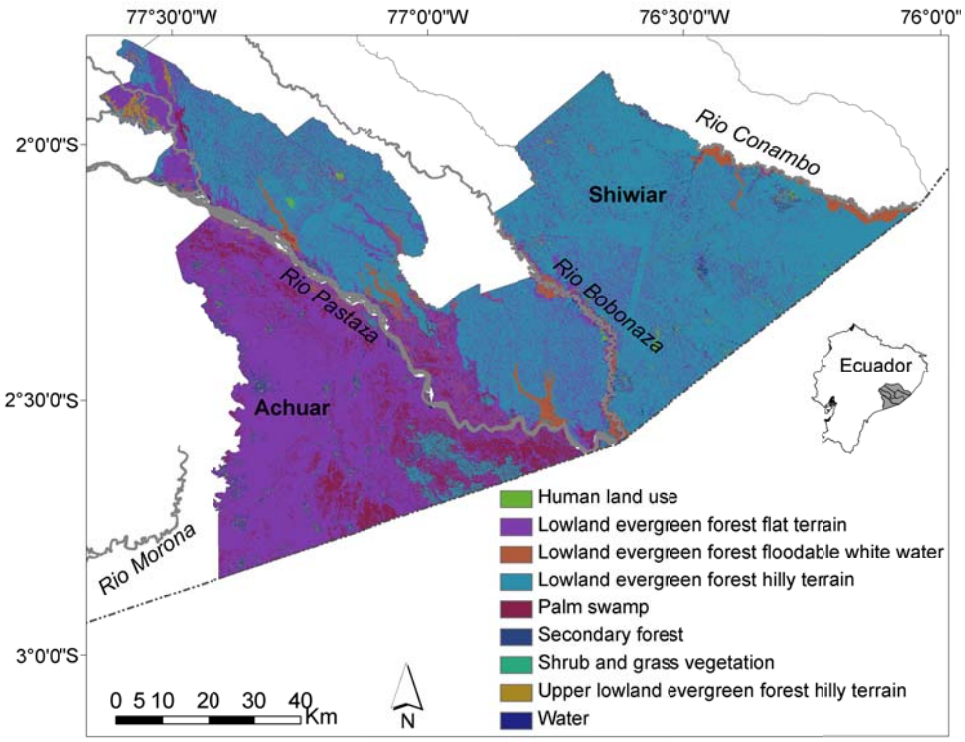


Figure 2.13. Detailed vegetation map of the Achuar and Shiwiar territories (GIS data source: Landsat ETM+ image classification by Lopez 2008). See Figure 2.4 for the locations of three 1-ha tree inventory plots.



Vegetation in the low terraces in the alluvial basins in Achuar corresponds to the "Amazon lowland white-water inundated evergreen tropical forests" category classified by Sierra (1999). Vegetation in the high terraces in Achuar that consist of ferralitic red soil corresponds to the "Amazon lowland evergreen forests" category on hilly terrain (Sierra 1999). Likewise, vegetation type found in the recent alluvial terraces and swampy alluvial floodplains with large inundated depressions in Achuar also corresponds to the "Amazon lowland evergreen forests" category (Lopez 2008). Vegetation of the high inter-fluvial alluvial terraces in Shiwiar corresponds to the "lowland evergreen tropical forest" category in hilly areas (Sierra 1999).

Lopez (2008) classified the vegetation and land cover types in the Achuar and Shiwiar territories based on a Landsat ETM+ image at a 30-m resolution. The Achuar territory is dominated by lowland evergreen forests on flat terrain and in floodable white water areas (Illustration 2.5A, 2.5B). The northwestern corner of Achuar contains some lowland and upper lowland evergreen forests on hilly terrain. Achuar has large areas of palm swamps. Human land use areas occur around indigenous communities and especially around households. Secondary vegetation usually coincides with the human land use areas. In contrast, the Shiwiar territory is dominated by lowland evergreen forests on hilly terrain. There is a lot less coverage of lowland evergreen forests on flat terrain and in floodable white water areas, and no palm swamps. In Shiwiar lands there are sporadic small patches of shrub and herb vegetation near the border to Peru. The distribution pattern of human land use areas and secondary vegetation is similar to Achuar (Lopez 2008). This dissertation aims to produce another vegetation and land cover classification that covers the Achuar, Shiwiar, Zapara and partial Kichwa territories by using four pan-sharpened Landsat ETM+ images with a 15-m resolution with object-based classification method.

Illustration 2.5. Aerial views of lowland evergreen forests by the rivers.

A.

B.

Conservation

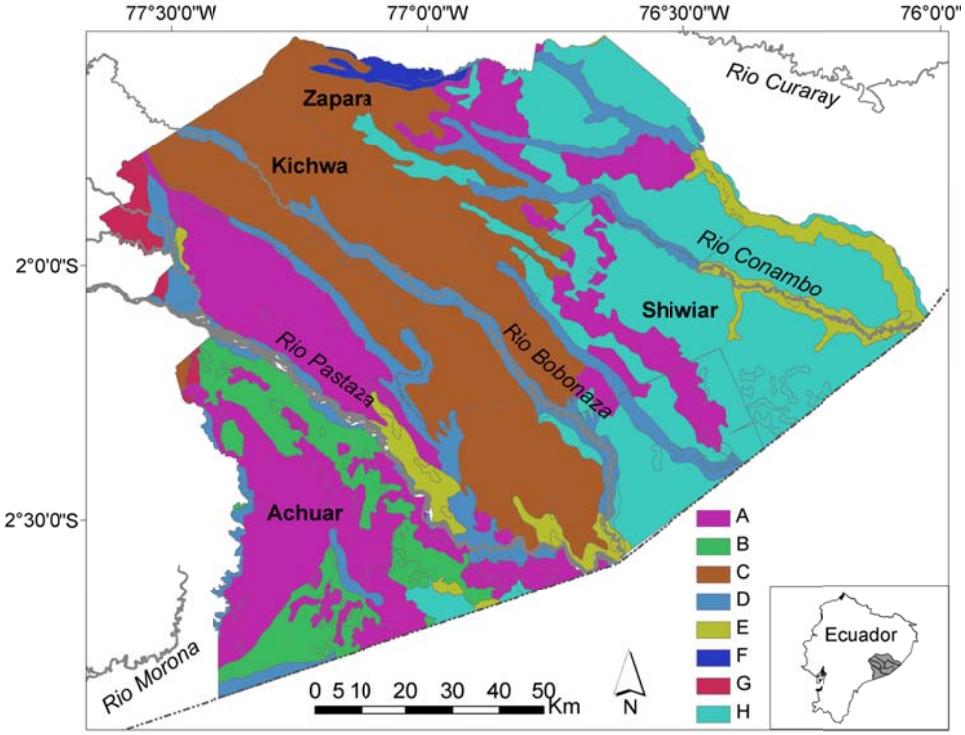
The Ecuadorian Amazon contains 11 tree species that are critically endangered, endangered, or vulnerable according to the International Union for Conservation of Nature and Natural Resources (IUCN) Redlist of Threatened Species (IUCN 2007).

The study region belongs to the part of the Amazon that is classified as one of the world's high-biodiversity wilderness areas by Conservation International. The Amazon has a great percentage of endemic plant species, low human population density, and is among the last places where indigenous people reside. It also supports great ecosystem services such as watershed protection, climate regulation, pollination, and carbon sequestration (Mittermeier et al. 2003). In addition, World Wildlife Fund (WWF) has identified the Amazon River and its tributaries as The Amazon River and Floodplain Ecoregion for ensuring full habitat representation, maintaining lateral and longitudinal terrestrial and aquatic connectivity, preserving hydrological and sedimentation cycles, and maintaining viable persistence of endemic and economically important species (WWF 2005). Hence, the Amazon urgently needs zonation maps that take both biodiversity persistence and sustainable natural resource management into consideration.

The study area is not included in any of the Ecuadorian protected forests, biological or ecological reserves, national parks, or biosphere reserves. However, a national map for forestry proposed eight types of land management in the study area: 1) complete protection of existing vegetation cover (A), 2) complete protection/area for cultivation with regulation in fertilization, inundation, and drainage (B), 3) complete protection/forested terrain for forest protection and reforestation (C), 4) terrain area for cultivation with control in fertility, aluminum content, and inundation (D), 5) terrain area for pasture with adequate drainage (E), 6) forested terrain for cultivation including protected forest and production under control in soil fertility and erosion (F), 7) forested

terrain area for pasture or cultivation including protected forest and extensive cattle raising under intensive control (G), and 8) forest terrain area for cultivation including forest for protection and production (H) (Figure 2.14).

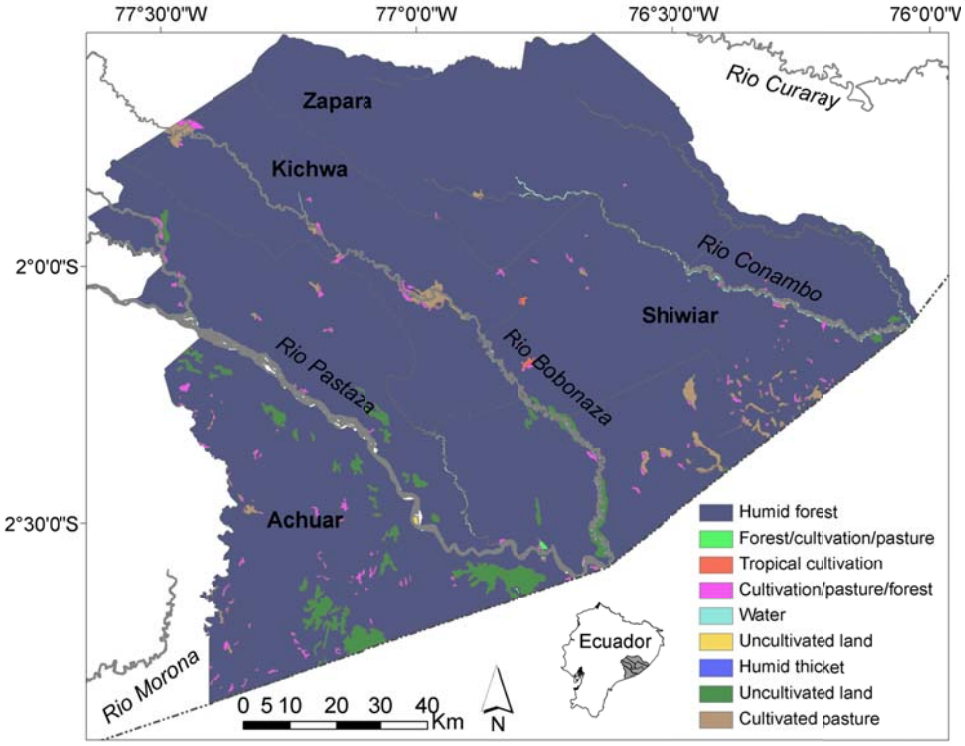
Figure 2.14. Proposed potential forestry plan for the study area. See the text for figure legend (GIS data source: Ministry of Environment in Quito, Ecuador (2000-2004) and provided by R. Sierra). See Figure 2.4 for the locations of three 1-ha tree inventory plots.



An actual national land use map produced by Centro de Levantamientos Integrados de Recursos Naturales por Sensores Remotos (CLIRSEN 2003) in Ecuador indicates that the study area comprises humid forests, forests with some cultivation and pasture, tropical cultivation, cultivation within pastures and forested areas, water, uncultivated lands, humid thickets, human land use, and cultivated pastures (Figure 2.15).

Figure 2.14 and 2.15 are based on potential forest estimates and actual land use classification of the entire Ecuador in a coarse scale. Therefore, the schemes and distribution of different land types are not specialized for the study area. My dissertation will employ analysis for conservation based on classified Landsat ETM+ pan-sharpened images and other remote sensing data, in order to provide technical recommendations for land use and natural resource management.

Figure 2.15. CLIRSEN land use map of the study area (GIS data source: CLIRSEN around 2003, provided by R. Sierra). See Figure 2.4 for the locations of three 1-ha tree inventory plots.



Realizing the importance of land management, and sustainable development and the necessity of systematic conservation planning, the political representatives in the

area—NAE, NASHIE, and La Nacionalidad Zapara de Ecuador (NAZAE)—took initial steps. The Center for Conservation in Indigenous Lands in the Western Amazon (CILWA) at the University of Texas and Fundación Ecuatoriana de Estudios Ecologicos (EcoCiencia) in Ecuador established collaborative projects with Achuar in 2000 and with Shiwiar and Zapara in 2003 for regional multiscale and multi-disciplinary conservation projects (R. Sierra, personal communication, 2006). Funding from various institutions including the University of Texas and the Gordon and Betty Moore Foundation was provided to support this initiative. My dissertation helps to provide technical recommendations for conservation planning from an ecological perspective.

WESTERN AMAZON

The study area in western Amazon corresponds to part of eastern Ecuador and part of northern Peru. The one-ha tree inventory plots in the Ecuadorian and Peruvian Amazon are located between 5-0°S and 77-73°W. In addition to the three tree 1-ha inventory plots in southeastern Ecuador, 34 one-ha plots in the Orellana and Sucumbios provinces of Ecuador (data obtained from N. Pitman) and 12 one-ha plots in the Loreto region of Peru (data provided by O. Phillips) are included in this western Amazonian species diversity study. All plots in northern Ecuador belong to the Rio Napo drainage basin, whereas the plots in Peru spread among the basins of Putumayo, Napo, Amazonian interbasin, Nanay, and lower Ucayali (Figure 2.16). Elevation of the 49 plots ranges from 94-305 m along a gradient that increases from the Loreto plots to the plots in northeastern Ecuador (Figure 2.17). Likewise, slope at the plots increase from almost flat terrain (0.4°) to very gentle hills (9°) (Figure 2.18).

Figure 2.16. Map of the region in western Amazon where the 49 one-ha tree inventory plots are located. Different symbols of the plots represent plot coordinators. This map also presents major rivers (in italic) and major drainage basins (in bold) (GIS data sources: Instituto Geográfico Nacional (IGN) in Lima, Peru (2004) and provided by R. Sierra, J. Postigo, and D. Salisbury).

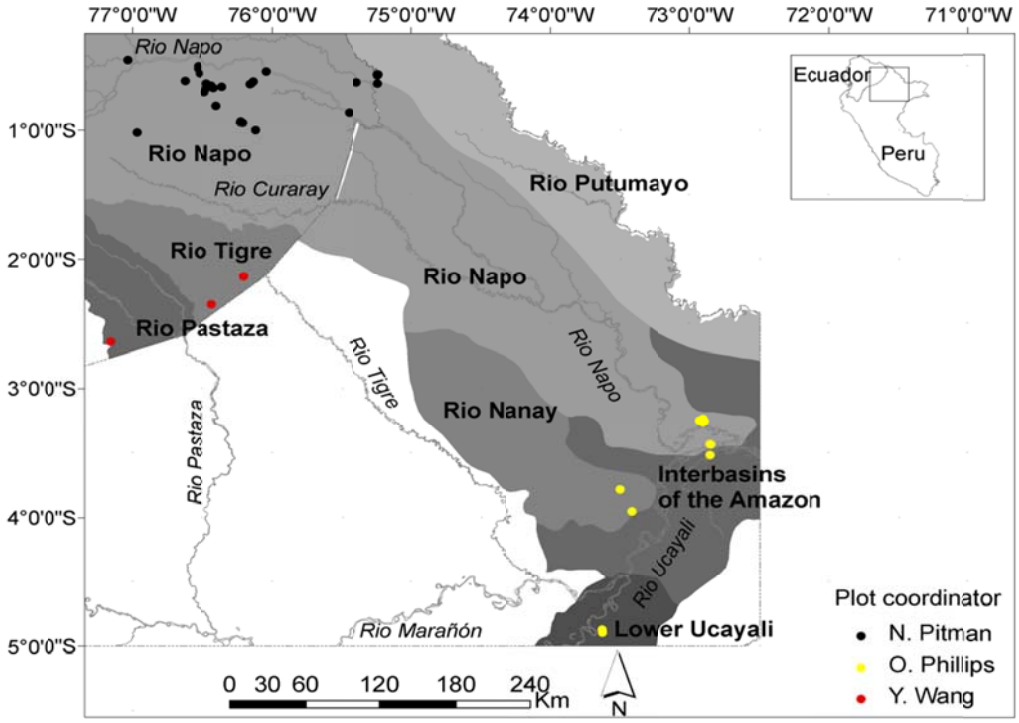


Figure 2.17. Elevation of the 49 one-ha plots and their surrounding areas in western Amazon (elevation data obtained from SRTM).

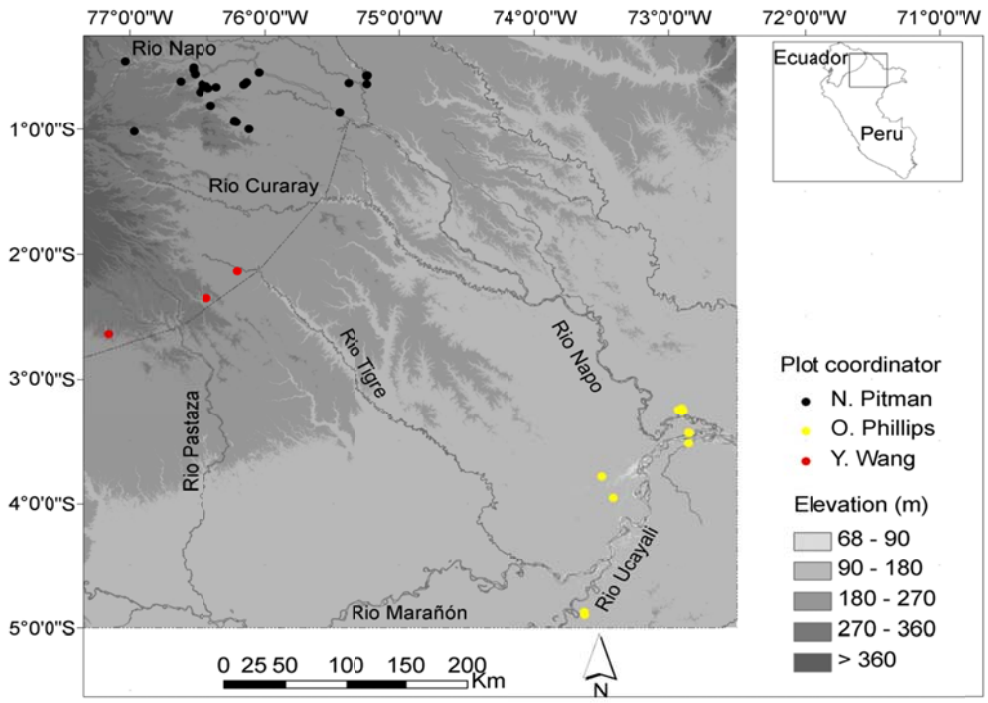
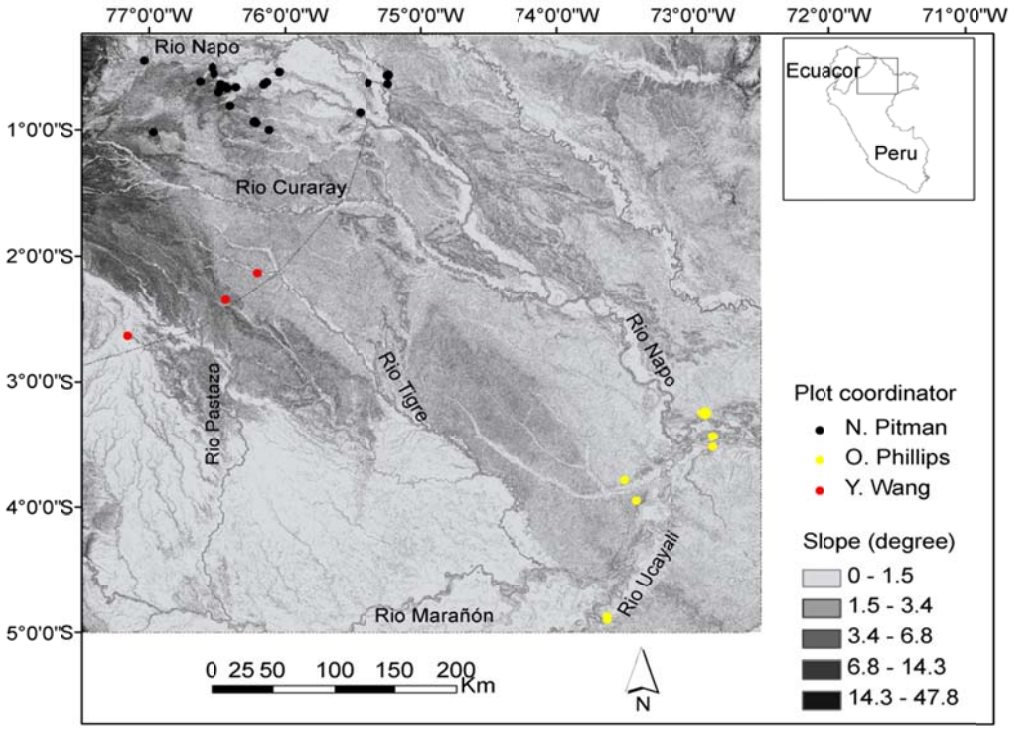


Figure 2.18. Slope (in degrees) of the 49 one-ha plots and their surrounding areas in western Amazon (slope data derived from SRTM).



Temperature among the 49 plots shows great homogeneity in annual mean temperature (24.7-26.8°C), mean diurnal range (9.3-10.1°), and annual range (11.1-12.2°). In contrast, the quantity and distribution of precipitation indicate great heterogeneity among the plots. Overall, plots in Loreto have lower annual rainfall (< 3,000 mm) compared to the Ecuadorian plots, among which the plots in the Rio Napo basin have the highest annual precipitation (Figure 2.19). These plots also have a broad range of precipitation seasonality. The driest months for some plots occur in December or January, but some plots have the least rainfall in August. The Sawastian plot in southeastern Ecuador has the lowest precipitation seasonality and a monthly rainfall

between 188-255 mm, whereas the Yarina plot has the highest precipitation seasonality and a monthly rainfall between 136-317 mm (Figure 2.20).

Figure 2.19. Annual precipitation (mm) of the 49 one-ha plots and their surrounding areas in western Amazon (precipitation data obtained from WorldCLim).

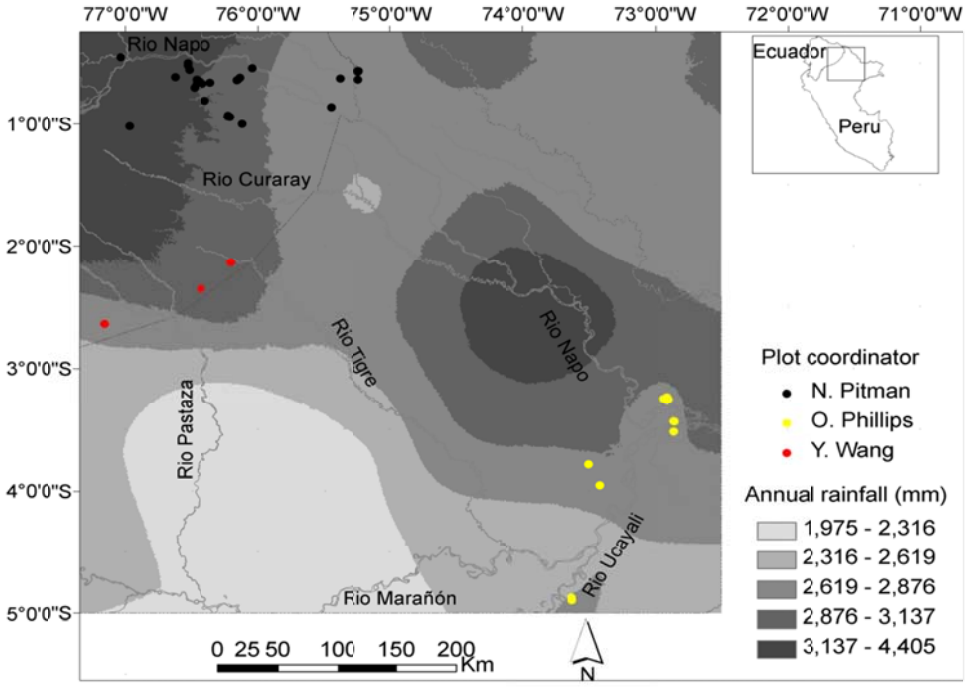
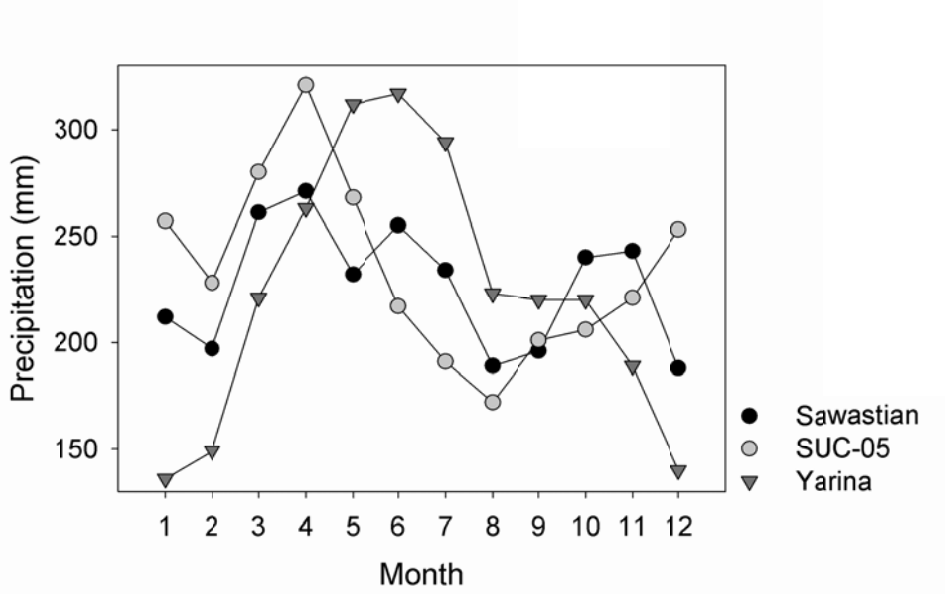


Figure 2.20. Comparison of monthly precipitation among three tree inventory plots (precipitation data obtained from WorldClim).



The Ecuadorian and Peruvian plots do not differ much from a geological perspective. The areas where the 49 plots are located comprise geological layers from Quaternary (Holocene and Pleistocene) and Neogene in Tertiary (Pliocene and Miocene) (Figure 2.21). Similarly, both Ecuadorian and Peruvian plots have disturbed vegetation, floodable riverine forests, lowland evergreen forests, and black-water palm forests (Figure 2.22). The soil composition consists of relatively nutrient-rich clay and relatively nutrient-poor sand and sandstone (Pomara 2009).

Figure 2.21. Geology layers of the 49 one-ha plots and their surrounding areas in western Amazon (GIS data sources: source for Figure 2.7 and Centro de Datos para la Conservación (CDC-UNALM) in Lima, Peru (2000-2004) and provided by R. Sierra and L. Pomara).

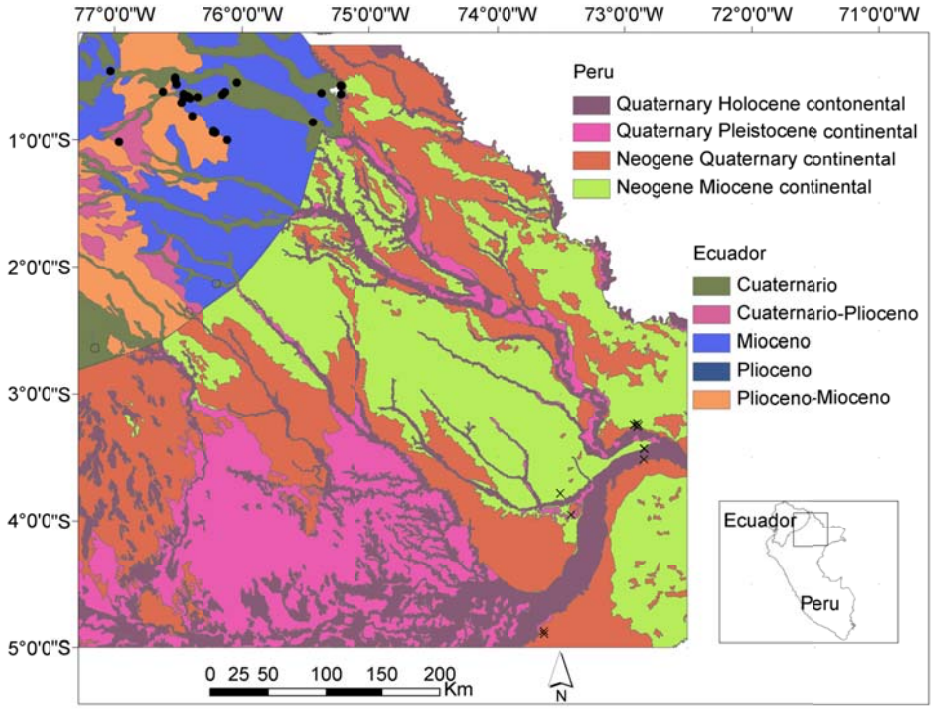
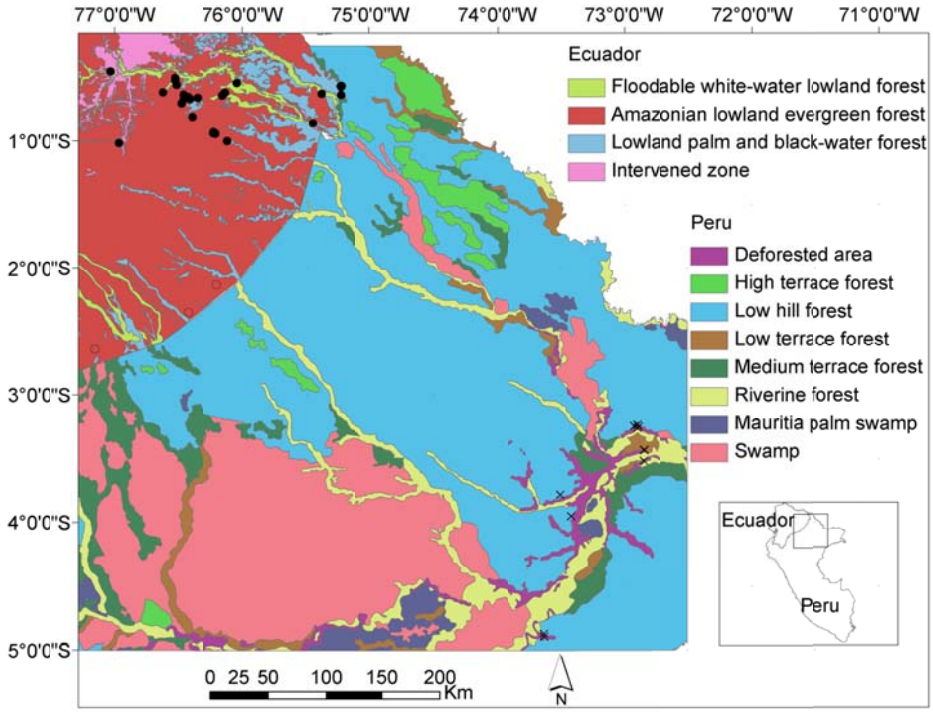


Figure 2.22. Vegetation types of the 49 one-ha tree inventory plots and their surrounding areas in western Amazon (GIS data sources: Sierra 1999 and Centro de Datos para la Conservación (CDC-UNALM) in Lima, Peru (2000-2004), provided by R. Sierra and L. Pomara).



Chapter 3: Methods

DATA ACQUISITION

Three 1-ha (100 X 100 m) tree inventory plots were established in 2006 in the Juyuintsa, Yutsuntsa, and Sawastian indigenous communities in southeastern Ecuador (Illustration 3.1, Table 3.1). The plot data taken included abundance, number of species, and size structure of all trees with at least 10 cm diameter at breast height (DBH) for their diameter, height, identification (Condit 1998), geographic coordinates of the plots with global positioning system (GPS), and locations of all documented trees by manual mapping and assigning spatial coordinates (Illustration 3.2A, 3.2B, 3.2C). Field voucher collection and species identification were conducted by Milton Tirado, an Ecuadorian botanist who has worked in the Amazon for many years. Rapid identification of trees that could be identified to species level first was conducted in the field during tree inventories, and was followed by another visit for voucher collection of trees that were previously identified to family/genus level or to morphospecies. Thorough voucher identification was done by comparing specimen in the National Herbarium of Ecuador (QNCE) in Quito, Ecuador. Each of the three 1-ha tree inventory plots has respectively 622, 610, and 555 tagged individuals that included 279, 237, and 148 species/morphospecies. I documented soil temperature, moisture, and texture/color along with slope and elevation readings from a GPS unit at each 20 X 20 m grid point during a revisit in Juyuintsa and Sawastian in 2008. Hence, in each plot there were 36 soil and topography readings. I was unable to return to Yutsuntsa in 2008 due to the lack of community permission, and therefore soil and topography data were not available for this site.

Illustration 3.1. Field crew in Sawastian in summer 2008.

Illustration 3.2. Identifying (A), measuring DBH (B), and tagging trees (C). Photos taken by Kenneth R. Young.

A.

B. C.

Hemispheric photographs, taken in 2006 for Yutsuntsa and in 2008 for Juyuintsa and Sawastian produced measures of the light environment at every 20 X 20 m grid point in each plot (Illustration 3.3). The camera settings were based upon trial and error in the field and recommendations from protocols used in other rainforest plots (M. Theobald 2004 and S. Patino 2005, unpublished data). I set a Canon Powershot S5-IS digital camera with a Phoenix 0.25X Super Fisheye converter on a tripod 1 m above ground, leveled horizontally with a bubble level. A white tag attached to the lens indicated the magnetic north direction. The focal length at autofocus, exposure mode and compensation, and sensitivity were set to be 6 mm, aperture priority, -0.7 eV, and ISO 400, respectively (Figure 3.1). I saved the images in the size of 3264 X 2448 pixels with fine compression quality and then computed percent canopy openness and leaf area index in Gap Light Analyzer (GLA) version 2.0 (Frazer et al. 1999).

Illustration 3.3. Taking hemispheric photographs. Photo taken by Kenneth R. Young.

Figure 3.1. An example of a hemispheric photograph.

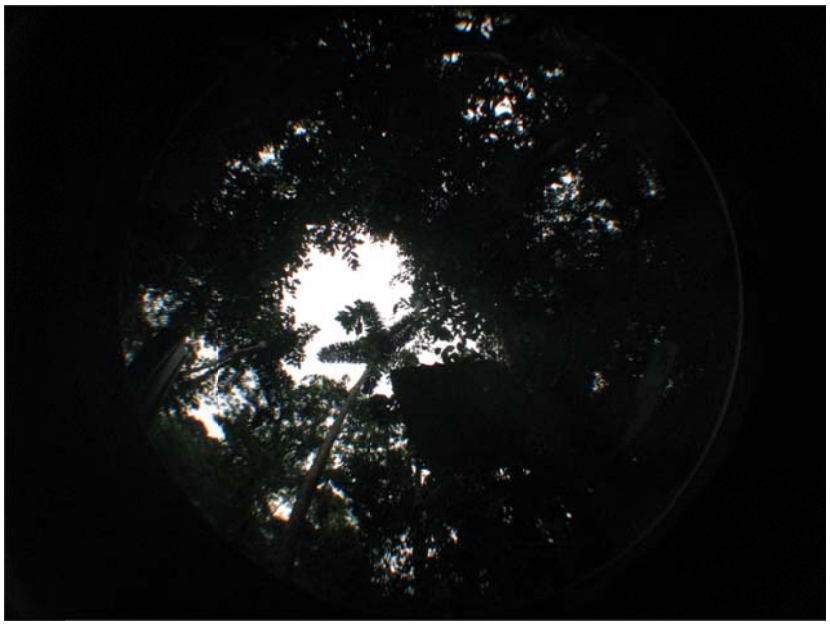


Table 3.1. Summary of the environmental attributes of the three 1-ha plots. Data were obtained from field measurements and sources for Figure 2.2, 2.4, 2.5, 2.6, 2.7, 2.8, 2.10, 2.13, and 2.15).

Attributes	Yutsuntsa	Juyuintsa	Sawastian
Year established	2006	2006	2006
Geographic coordinates (in decimal degrees)	-2.35, -76.43	-2.13, -76.2	-2.64, -77.15
Elevation (m)	265	205	250
Slope from field data (degrees) (range, mean)	N/A	5-20, 11.75	2-20, 12.58
Annual mean temperature (°C)	25.4	25.6	25.5
Annual precipitation (mm)	3,009	2,988	2,718
Percentage canopy openness (%) (range, mean)	7-8.5, 7.9	6.2-9.2, 7.5	7-12.6, 9.5
Drainage basin	Rio Tigre	Rio Tigre	Rio Pastaza
Primary soil type	K	K3	K6
Primary geological formations	Quaternary-Pliocene mesa, volcanic sediments	Miocene Curaray with Clay	Recent Quaternary alluvial deposits
Primary geomorphological formations	Half-alluvium	Peri-Andean slopes with sandstone/clay	Piedmont
Soil moisture (%) (range, mean)	N/A	20-58, 41	20-58, 40
Soil temperature (°C) (range, mean)	N/A	18-22.5, 20	20-22, 21
Primary vegetation type	Lowland evergreen forest on hilly terrain	Lowland evergreen forest on hilly terrain	Lowland evergreen forest on flat terrain
Euclidean distance to community center (km)	2.9	1.6	0.8

In addition to the above three plots, the other 1-ha Amazonian plot data I used included species names and number of stems in 34 plots in northeastern Ecuador (provided by N. Pitman) and 12 plots in Loreto, northern Peru (provided by O. Phillips). Only 1-ha plots that documented trees ≥ 10 cm DBH are used here. These 49 plots are located in an area that is approximately 475 (east-west) by 480 (north-south) km (Figure 2.17 in Chapter 2: Study Area). The biophysical environment data layers for the 49 plots were derived from two databases. A digital elevation model (DEM) derived from NASA's Shuttle Radar Topography Mission (SRTM) was acquired from United States Geological Survey (USGS) in a 90-m resolution. I created slope, aspect, and compound topographic index (CTI) layers from this DEM. WorldClim (http://www.worldclim.org/) is a set of climate data layers with a spatial resolution of 1 km. Variables in the data layers include 19 derived bioclimatic variables, monthly precipitation and the average, maximum, and minimum of monthly temperature (Hijmans et al. 2005).

R. Sierra obtained digital videos with a Sony TRV900 digital camcorder across four flight lines in the study region and recorded still images in September 2006 (Figure 3.2) (Red Hen Systems, Inc.). The four flight lines were drawn along gradients of topographic heterogeneity of the study area. The videos, taken in the mornings, were georeferenced via a Video Mapping System (VMS 200). This system translated the GPS radio signals into sounds and was used to index the video frames with coordinates. The video positions were post-processed in the software Media Mapper. S. Lopez used the video index as the reference data by matching the times of the GPS with the times on the video. The center of a video scene corresponded to only one GPS location (Lopez 2008). GPS points were collected every second. Theoretically there were 24 frames per second. However, only one of these frames contained the exact time of the GPS point and that became the frame used for creating photomosaics and for the georeferencing process. The

numbers of points used for georeferencing a mosaic depended on how many still images were used for creating a mosaic (Lopez 2008). The 52 mosaicked aerial photographs varied in size, as they contained approximately 5-10 still images per photograph and each still image was approximately 125-185 m X 100-120 m. The root mean square (RMS) error for those transect mosaics was around 14.5 m. Georeferenced and merged photomosaics that were derived from the still images contain a resolution of 5 cm (S. Lopez, personal communication) (Illustration 3.4). M. Stojic (2004) has written detailed instructions for this method (ftp://updates.lggm.com/Updates/Web/FocusOn).

Figure 3.2. The 52 mosaicked aerial photographs (in red circles), 18 aerial photomosaics, and locations of three community centers (in red triangles). The three 1-ha tree inventory plots did not overlap with any aerial photograph.

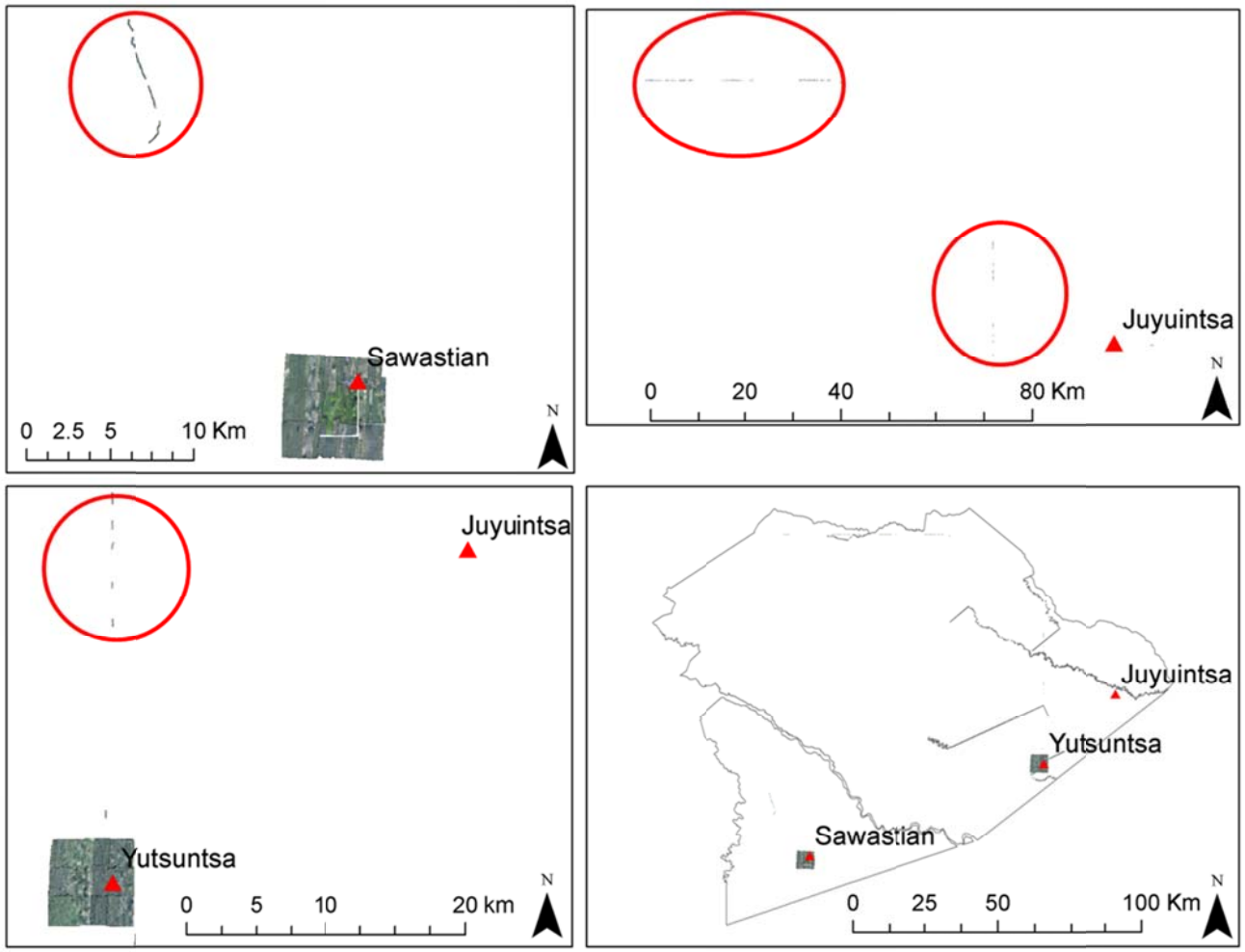


Illustration 3.4. An example of aerial photographs in a 5-cm resolution.

Between late 2005 and early 2006 S. Lopez collected aerial photographs with a Nikon D2X still camera within an area of 6 X 6 km for seven indigenous communities with 32 flight lines separated by 180 m intervals (Figure 3.2). Flyovers occurred at a height of 500 m aboveground. GPS and a video mapping system (see above) were used for collecting the positional information. A GPS base station was established in Puyo at 1.48°S, 78.003°W, and 958.9042 m above sea level. Images were geometrically corrected using differentially corrected GPS data and a third order polynomial transformation (Lopez 2008, S. Lopez, person communication). The original RMS error of the

photomosaics ranged between 10 and 15 m. With the aid of differentially corrected ground control points, the mosaics' errors were reduced to approximately 5 m. Nine preliminary photomosaics of undisturbed, forested, residential, agricultural, and pasture areas were created with a spatial resolution of 10 cm in each of the seven selected communities (Lopez, 2008). I only used the photomosaics from the Yutsuntsa and Sawastian communities in my dissertation (Illustration 3.5).

Illustration 3.5. An example of aerial photo mosaics in a 10-cm resolution.

These high-resolution images provided details for palm species identification and canopy shadow mapping. For vegetation and habitat mapping, two types of images in a relatively coarser resolution were available. The Landsat 7 spacecraft of the ETM+ sensor was launched in 1999, with six multispectral bands (0.45-2.35 μm), one thermal band (10.4-12.5 μm), and one panchromatic band (0.52-0.9 μm). The resolution includes 15 m (panchromatic band), 30 m (visible, near infrared, and mid infrared bands), and 60

m (thermal band) (NASA 2006). Four Level 1T (standard terrain correction) ETM+ scenes from September, October, or November in 2002, obtained from United States Geological Survey (USGS), cover the entire study region and contain the least cloud cover. Georeferenced images obtained by the Visible and Near Infrared (VNIR) subsystem of the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Level 2 (ASTER09) in 2002, 2003, and 2006, collaborated by NASA and Japan's Ministry of Economy Trade and Industry (METI), cover almost the entire study area with three bands (near infrared, red, and green) in a 15-m resolution. The vegetation and habitat classifications for my dissertation were conducted using the pan-sharpened ETM+ images and employed accuracy assessment using the ASTER images as references.

DATA ANALYSIS METHODS

Alpha diversity and forest structure in the Ecuadorian Amazon

Species diversity and distribution patterns

One of the essential questions in terms of understanding tree diversity patterns at the local scale (i.e. alpha diversity) is to what extent difference in species composition is associated with neutrality, habitat heterogeneity, or dispersal limitation. To estimate similarity in species composition among the three 1-ha inventory plots, I compared the vouchers of morphospecies in the National Herbarium of Ecuador in Quito, Ecuador in summer 2008 to determine where or not a morphospecies from one plot differed from a morphospecies of the same temporary identification from another plot. As a result, I assigned morphospecies with a common identification if a morphospecies occurred in more than one plot and with a unique identification if a morphospecies only occurred in a specific plot.

The forest communities were characterized on the three 1-ha Ecuadorian plots in terms of their species richness, species composition, and genus composition. Species composition was informed using both species abundance and presence/absence data. At the genus level, I only used genus abundance (i.e. number of stems) to examine community composition because a preliminary analysis indicated that no prominent compositional patterns were detected using genus presence/absence data. A robust measure that previous studies in the Amazon have used is Fisher's alpha diversity index (e.g. Pitman et al. 2002, Phillips et al. 2006, Davidar et al. 2007). In addition to Fisher's alpha diversity index (Hayek and Buzas 1996), Shannon diversity index in natural logarithms (Magurran 2004) and Simpson inversed diversity index (Magurran 2004) were derived in EstimateS 8.2.0 (http://viceroy.eeb.uconn.edu/estimates). Each computation comprised 100 randomized iterations (Colwell and Coddington 1995).

Distance matrices were constructed for exploring site-to-site floristic dissimilarity and the relationships between the biophysical environment and species/genus composition. This approach was taken because distance matrices provide a flexible format for multivariate data analyses. The floristic distance was measured using Sørensen (Bray-Curtis) index of similarity, a semimetric distance measure that has been well recognized in community ecology studies (McCune and Grace 2002), based on the abundance or presence/absence of the species or genus (Phillips et al. 2003a). Comparisons of floristic variation were conducted at within- and between-plot levels. The field sampling unit occurred at grids of 20 X 20 m and therefore, the within-plot floristic variation was compared among paired 25 grids. Having 555-622 stems in each plot, the within-plot comparisons used an average of approximately 22-25 stems per grid. The distance matrices based on environmental variables (i.e. light, slope, and soil

measurements) were based on the Euclidian distance, i.e. the difference in values between the paired within-plot grids of the three plots.

The aforementioned distance matrices were used in four analyses: 1) Non-metric multidimensional scaling (NMS) ordination for exploring floristic compositional patterns in each plot at both species and genus levels (Kruskal 1964, Legendre and Legendre 1998, McCune et al. 2002), 2) Mantel tests on correlation between floristic and environmental matrices (Mantel 1967, Legendre and Legendre 1998, McCune et al. 2002, Legendre and Lapointe 2004), 3) indicator species analysis for examining the degree of environmental association at both species and genus levels (Phillips et al. 2003a), and 4) multiple regression on distance matrices to model the species composition matrices (Legendre et al. 1994, Legendre and Legendre 1998, Tuomisto and Ruokolainen 2006).

As an exploratory tool, ordination was used for seeking and describing patterns and gradients of species composition. More specifically, NMS is an ordination technique based on a distance matrix that runs iterative searches for ranking and placement on dimensions (axes) that minimize the stress of the multi-dimensional configuration. Stress is a measure of departure from monotonicity in the relationship between the distance in the original multi-dimensional space and distance in the reduced multi-dimensional ordination space (McCune et al. 2002). NMS is well suited for community ecology data analysis because it suits data that are nonnormal and it uses ranked order of among-sample dissimilarities in distances measured in species space and in environmental gradients (Clarke 1993, McCune and Grace 2002). I conducted NMS in PC-ORD 5 (McCune and Mefford 1999) using the Sørensen distance matrices, with an initial six-dimensional solution, a step-down option to reduce the dimensionality, an instability criterion of 0.0005, 200 iterations, ten runs on the real data from random starting configurations, and 20 runs using Monte Carlo randomization tests of significance to

select the appropriate number of dimensions for each ordination (PC-ORD manual). With the decided number of dimensions that resulted in a stress < 20 as recommended by Clarke (1993), the final NMS run was performed with the best starting configuration, no step-down option in dimensionality, and one run with the real data (PC-ORD manual). PC-ORD also computed the correlations (rank Kendall's Tau) between the ordination axes vs. Sørensen floristic distance matrices or the environmental Euclidian matrices.

To address the importance of specific environmental factors that might contribute to alpha diversity patterns, correlation between distance matrices of species composition and the environment needed to be computed. In order to evaluate whether or not there was a significant relationship between paired distance matrices of species/genus composition and each environmental variable, I used the Mantel test in PC-ORD 5 (Phillips et al. 2003a, Phillips et al. 2006, Pomara 2009). Mantel tests seek linear relationships between two distance matrices constructed with any distance or similarity measures and therefore, provide great power and flexibility for ecological data analysis (McCune and Grace 2002). Each pair consisted of a Sørensen distance matrix and a Euclidian distance matrix of an environmental variable. The quantified environmental variables included percent canopy openness, leaf area index, soil moisture, soil temperature, soil pH, slope, soil color (based on the Munsell Soil Color Chart), and soil chroma read from the Munsell Soil Color Chart. The Mantel test evaluates the correlation between distance matrices in a way analogous to Pearson's correlation *r*, but it accounts for non-independence of matrix cells in the estimation of significance (Smouse et al. 1986, Legendre and Legendre 1998, McCune et al. 2002). A Monte Carlo procedure in the Mantel test estimated the probability of error by comparing the observed distribution of Mantel's *r* against the random distribution generated from permuting the actual

matrices and recalculating *r* for 999 times (Legendre and Legendre 1998, McCune et al. 2002, Legendre and Lapointe 2004).

On an exploratory basis, I examined the extent to which different species indicated environmental conditions as part of descriptions of species diversity patterns. To test the degree of habitat association at both species and genus levels at the level of the three 1-ha plots, I applied indicator species analysis in PC-ORD 5 (Phillips et al. 2003a, Pomara 2009). The objective of indicator species analysis was to detect simple, intuitive patterns of species grouping based on categorical environmental variables (Dufrene and Legendre 1997, McCune and Grace 2002). This method combines information on species or genus abundance in a particular environmental group and the constancy of a species in that particular group. It produces an indicator value for each species in each group and then tests for statistical significance of the indicator value using a randomization technique (Dufrene and Legendre 1997). For each environmental variable used in the Mantel test, I categorized it into two levels that represented the lower and higher values of the variable. I used the original categorical labels for the Munsell soil color and soil chroma. PC-ORD conducted 1,000 runs of a Monte Carlo randomization test to examine the statistical significance of the maximum indicator value recorded for a given species (McCune and Mefford 1999).

In addition to Mantel tests, I employed multiple regression on distance matrices that involves a response matrix on explanatory distance matrices of ecological or spatial similarities (Linchstein 2007). The method is flexible in its broad data type compatibility, as well as its ability to separate environmental distances into distinct distance matrices to allow inferences to be made at the level of individual variables (Linchstein 2007). For biodiversity studies, multiple regressions on distance matrices express the variation in one dependent matrix (i.e. species or genus floristic matrix) in terms of the variation in a

set of independent matrices (i.e. environmental variable matrix). Testing the significance of regression parameters employs Monte Carlo permutations (Legendre et al. 1994, Legendre and Legendre 1998, Tuomisto and Ruokolainen 2006). The environmental variables that were significantly correlated with tree species or genus composition in the Mantel tests were included as input variables in multiple regressions (e.g. Pomara 2009). The analysis was conducted using the ecodist package in R 2.10.1 (Goslee and Urban 2007), with 1,000 permutations and both forward selection and backward elimination methods (Legendre et al. 1994, Phillips et al. 2003a, Lichstein 2007).

Spatial point patterns of tree distribution

At the local scale, patterns of spatial distribution of individual trees can shed light on dimensions of species diversity patterns beyond gradients of similarity and direct associations with the environment. Spatial point patterns of trees may potentially elucidate the extent to which forest dynamics or species interactions contribute to local diversity. Variation in spatial patterns among different taxonomic groups may be the result of different dispersal mechanisms or varying responses of trees to disturbance history. Understanding of spatial point patterns of trees, even as exploratory forms of analysis, assists in enriching knowledge of biodiversity for future applications in conservation biogeography. To examine the level of dispersion of trees in a plot, I used number of stems in the 20 X 20 m grids in each plot. The dispersion indices used in the analysis included Index of Dispersion (PASSaGE manual), Green's Index (Green 1966), and Morisita's Index (Morisita 1959), which were sought to demonstrate level of spatial dispersion in variation of indices (Hurlbert 1990). Index of Dispersion refers to the ratio between the variance and mean of stem counts and is expected to equal 1 under a random distribution of points. Green's Index is the ratio between (Index of Dispersion - 1) and the

degree of freedom (n - 1, n = total number of grids). It varies between 0 for random distributions and 1 for maximally clumped distributions. Moristia's Index is the scaled probability that two randomly chosen points are in the same grid. A higher Morisita's Index indicates a more clumped distribution. All the dispersion indices were derived using PASSaGE 2 (http://www.passagesoftware.net/).

In this dissertation I also aimed to quantify the spatial pattern of local tree communities in order to collect information that may aid interpretation of tree diversity attributes (Cressie 1993, Woodall and Graham 2004). Spatial point pattern analysis can help refine understanding of ecological processes, such as life history of individuals in the forest (e.g. establishment, growth, competition, and mortality) (Hasse 1995, Dale 1999). More specifically, I employed spatial analyses that used point-to-point distances for two-dimensional descriptive statistics (Hasse 1995, Dale 1999). Ripley's K function (Ripley 1976, 1977), a widely used multi-distance spatial cluster analysis, was calculated for summarizing spatial dependence (clustering or dispersion) of trees over a range of distances within each plot (Getis and Franklin 1987, Condit et al. 2000, Perry et al. 2006). The changing spatial patterns at multiple distances reflect dominance of particular spatial processes at different ranges of neighborhood in a circle of radius d (Fortin and Dale 2005; Ripley 1977). Second-order point pattern analysis was conducted using PASSaGE 2 and K is estimated as

$$\hat{K}(d) = \frac{A}{n^2} \sum_{i=1}^{n} \sum_{j=1, j \neq i}^{n} w_{ij} k_{ij}$$

Where A is the area of the study plot, n is the number of points within the plot, w_{ij} is a weight for edge effects (see below), and k_{ij} is 1 if points i and j are at distance d or less apart from each other, or 0 otherwise (Dale 1999, Fotheringham et al. 2000, PASSaGE manual). Different versions of transformed Ripley's K have been suggested, for example,

in PASSaGE the transformed K is represented with L_{Hat}, as d - sqrt(K(d)/pi) (Dale 1999). L_{Hat} is 0 when points are randomly distributed; $L_{Hat} < 0$ indicates clumping while $L_{Hat} > 0$ indicates dispersion (Dale 1999, Fotheringham et al. 2000). L_{Hat} and its relative relationship to the L_{Hat} at complete spatial randomness (CSR) indicate whether the tree distribution at a particular distance is clustered ($L_{Hat} > L_{Hat}$ at CSR) or dispersed ($L_{Hat} < L_{Hat}$ at CSR). I computed L_{Hat} based on tree coordinates in each plot and a distance matrix derived from the Euclidian distance between trees. The computation calculated L_{Hat} for up to 25% of the maximum distance ranges between trees for every 2 m. I controlled the edge effects by weighing each tree point by the inverse of the proportion of the circle of radius d centered on a point that falls within the plot (the area/volume option as recommended in PASSaGE manual). I ran 99 iterations of a randomization test to construct the upper and lower 95% confidence limits. Distances for which the L_{Hat} is found outside of the confidence envelope are distances for where there is significant clustering or dispersion.

In addition to spatial clustering/dispersion across ranges of distances, biodiversity attributes include associations between individual trees. To examine spatial associations between trees over a range of distances within each plot, a $K_{1\text{-}2}(d)$ function was computed for second-order neighborhood analysis from a bivariate spatial point pattern (Lotwick and Silverman 1982; Fortin and Dale 2005). The combined $K_{1\text{-}2}(d)$ of the relationship between points of type 1 and type 2 is determined as (Upton and Fingleton 1985):

$$\hat{K}_{1\text{-}2}(d) = \frac{n_2 \hat{K}_{1,2}(d) + n_1 \hat{K}_{2,1}(d)}{n_1 + n_2}$$

$L_{1\text{-}2}(d)$ is a linear version of $K_{1\text{-}2}(d)$ as d - sqrt($K_{1\text{-}2}(d)$/pi), with an expectation of 0 under independence between points that belong to two categories (PASSaGE manual). A bivariate $L_{1\text{-}2}(d)$ represents the contrast or association between two categories of points,

either whether points of a specific category are associated (or disassociated) with points of the same category or with points of a specific different category. $L_{1\text{-}2}(d)$ becomes positive when points from the two categories show attraction (clustering) and negative when they show repulsion (dispersion). I computed the bivariate L_{Hat} with the same settings as above plus an additional randomization test of whether the association of all trees of canopy vs. canopy, subcanopy vs. subcanopy, or subcanopy vs. canopy indicated clustering (attraction between the two categories) or dispersion (repulsion between the two) (Goreaud and Pelissier 2003, Franklin et al. 2010).

In addition, spatial association between individual trees can be examined from a distance- or point-based view. I discuss an exploratory analysis using local Ripley's K in Chapter 4. Local Ripley's K was computed with an interest in examining and detecting individual trees that are spatially clustered or dispersed at a particular distance or changes in spatial patterns over multiple distances for a particular tree individual. Getis and Franklin (1987) developed a second-order spatial analysis by creating a local version of Ripley's K function with the i^{th} point in a spatial point pattern:

$$L_i(r) = \sqrt{\frac{a}{(n-1)\pi} \sum_j e_{ij}}$$

Where the sum is over all *i* and all *j* that lie within a distance *r* of the i^{th} point, *a* is the area of the observation window, *n* is the number of points in the spatial point pattern, and e_{ij} is an edge correction term (Help file for spatstat package in R). The value of $L_i(r)$ can also be interpreted as one of the summands that contribute to the global estimate of the L function (Help file for spatstat package in R). Furthermore, when a bivariate local Ripley's K is computed, the result may reveal ecological interactions between two groups of trees in different taxa (family, genus, or species) or size/height classes at different

neighborhoods in the study region. This computation was not included in the dissertation study, but will be examined for future research.

Identifying biodiversity patterns aids understanding of ecological processes. Ecological data are often characterized by spatial patterns caused by the magnitude, intensity, and extent of spatial autocorrelation (Fortin et al. 2002). To obtain an overall pattern of global spatial autocorrelation of tree diameter (DBH) and height, I computed global Moran's I and Geary's C indices using PASSaGE 2. Both indices estimate spatial intensity and scale of quantitative data from noncontiguous sampling units. Moran's I (Moran 1950) measures global spatial autocorrelation to detect spatial patterns departing from randomness:

$$I = n\frac{\sum_{ij} w_{ij}(y_i - \bar{y})(y_j - \bar{y})}{W\sum_{i=1}^{n}(y_i - \bar{y})^2}$$

Where y_i or y_j is the value of the variable (DBH or height) at the i^{th} or j^{th} location, n is the number of points, w_{ij} is a weight indicating the spatial relationship of points i and j, $\sum_{ij}$ indicates the sum over all *i* and all *j* where, and $W = \sum_{ij} w_{ij}$ as the sum of weights (Moran 1950, PASSaGE manual). Positive Moran's I indicates positive spatial autocorrelation whereas negative Moran's I indicates negative spatial autocorrelation. Geary's C (Geary 1954) is essentially a standardized semivariogram that ranges from 0 to infinity, with an expected value of 1 under no spatial autocorrelation:

$$c = (n-1)\frac{\sum_{ij} w_{ij}(y_i - y_j)^2}{2W\sum_{i=1}^{n}(y_i - \bar{y})^2}$$

Geary's C between 0-1 indicates positive spatial autocorrelation whereas Geary's C > 1 suggests negative spatial autocorrelation (PASSaGE manual). Moran's I and Geary's C yield similar interpretations, but Moran's I is produced by standardizing the spatial autocovariance by the variance of the data values whereas Geary's C uses the sum of the squared differences between pairs of data values as its measure of covariation (Sokal 1979). Therefore, Moran's I computes the degree of spatial autocorrelation as a function of spatial lags whereas Geary's C measures the difference among values at nearby locations (Fortin et al. 2002). Using both Moran's I and Geary's C and yield compatible, or sometimes different but complementary results (Rosenberg et al. 1999). I computed Moran's I and Geary's C by using ten distance classes, an inverse distance weighting (Jumars et al. 1977), and 999 permutations for a randomization test.

In the Results and Discussion chapter for alpha diversity I demonstrate an exploratory analysis aiming to elucidate patterns of local spatial autocorrelations for tree DBH and tree height. While global Moran's I describes an overall spatial pattern in the study region, Local Spatial Autocorrelation (LISA) using Anselin's local Moran's I (Anselin 1995) detects local spatial autocorrelation by identifying local clusters (regions where adjacent areas have similar values) or spatial outliers (areas distinct from their neighbors in terms of the values):

$$I_i = \frac{\left(y_i - \bar{y}\right)\sum_{j=1}^{n} w_{ij}\left(y_j - \bar{y}\right)^2}{m_2}$$

Where m_2 is the average of the squared deviations from the mean:

$$m_2 = \frac{\sum_{j=1}^{n}\left(y_j - \bar{y}\right)^2}{n}$$

LISA decomposes Moran's I into contributions for each location in the study region. The sum of local Moran's I for all observations is proportional to global Moran's I (Anselin

1995). I computed univariate LISA for examining the local spatial clustering for trees of different diameters (DBH) and heights using OpenGeoDa 0.9.8 (Anselin et al. 2002) (http://geodacenter.asu.edu/). Computing the LISA statistics required generating a spatial weight profile. OpenGeoDa created a distance-based spatial weight for each plot using an internally created threshold distance, which was the minimum distance required to assure that each observation had at least one neighbor (GeoDa 0.9 User Guide 2003). The LISA statistics was conducted with a randomization test in 999 permutations at a significance filter of $p < 0.05$. In addition, a bivariate version of LISA for tree DBH and height is suggested for future research in the Discussion chapter:

$$I_{kl}^{i} = z_k^i \sum_j w_{ij} z_l^j$$

For the value x of variables k and l, $z_k = [x_k - mean\ (x_k)]/\sigma_k$ and $z_l = [x_l - mean\ (x_l)]/\sigma_l$ (Anselin et al. 2002).

Beta diversity patterns in eastern Ecuador and northern Peru

Understanding biodiversity patterns and ecological processes often involves researching more than one scale and spatial extent. Mechanisms that contribute to local-scale biodiversity patterns may show similarity or dissimilarity to what affect regional biodiversity, under the influence of geographic distance, climate, or geology. The next step after examining alpha biodiversity patterns was to compare and contrast patterns observed at the local scale to the regional scale. In this dissertation I aimed to conduct species beta diversity analyses paralleled to the alpha diversity study, except for the spatial point pattern analysis due to the lack of precise tree locality data in western Amazon. The floristic comparisons among the three 1-ha plots in southeastern Ecuador included unknown and morphospecies because I was able to compare vouchers at the

herbarium in Quito to differentiate morpho and unknown individuals. However, I did not have access to vouchers collected from the plots in northeastern Ecuador and Peru from the research efforts of N. Pitman and O. Phillips. The analysis of the tree species inventory data in northeastern Ecuador (34 plots), southeastern Ecuador (three plots), and Loreto, Peru (12 plots) only included plot species with species-level identification in order to avoid any confusion originating from determining if morpho-species from different plots were conspecific. The analyses were conducted with two sets of plot data: 49 one-ha plots and a subset that included 37 one-ha plots that were located in non-flooded ("terra firme") forests after eliminating plots that contained indicative species of floodable or swamp forests.

To examine how floristic composition differed between paired plots, I constructed Sørensen's dissimilarity distance matrices for all 49 plots and 37 subset plots using abundance data at both species and genus levels (see above). To elucidate whether or not plots in these regions form clusters in the ordination space, I applied Non-metric Multidimensional Scaling (NMS) ordination using Sørensen's similarity distance matrix based on species and genus abundance (see above). Species similarity indices against distances between paired plots and total number of sampled species were used to demonstrate how species diversity patterns (beta diversity) vary with geographic distance and sample size (Condit et al. 2000, Pyke et al. 2001).

In addition, I employed the Mantel tests, indicator species analysis, and multiple regressions to elucidate whether or not and to what extent the regional habitat variables affect floristic composition at both species and genus levels from the 49 plots and 37 subset plots (see above). The habitat variables included 19 bioclimatic variables that were derived from WorldClim (http://www.worldclim.org/), monthly temperature (from WorldClim), monthly precipitation at its minimum, maximum, and mean (from

WorldClim), elevation (from SRTM), slope, aspect, and compound topographic index (CTI). Slope, aspect, and CTI layers were derived from the elevation layer. I processed these 71 raster data layers in ArcGIS 9.3.1 (ESRI Inc.) to extract the variable values at the plot locations in Ecuador and Peru.

Remote sensing-based canopy palm and canopy opening distribution patterns

Extraction of canopy shadows and accuracy assessment

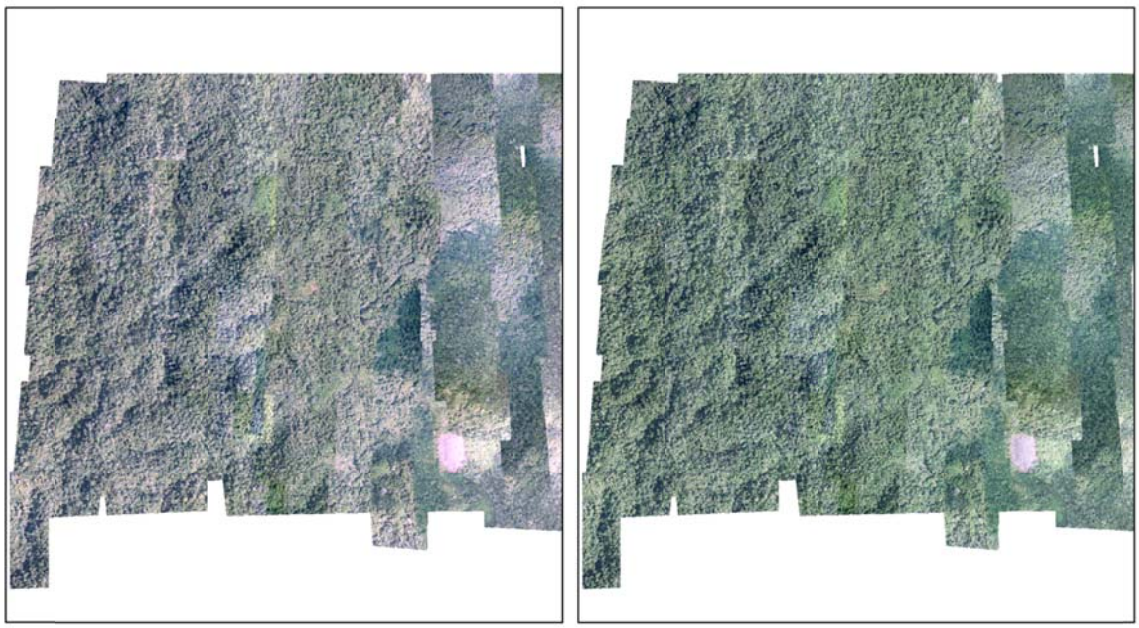
Examining patterns and mechanisms for alpha diversity aids understanding of the horizontal dimension of biodiversity components. Another dimension of biodiversity features the vertical perspective of forest structure. Tree community structural elements such as canopy gaps, canopy profiles of height and crown size, or tree stand diameter, constitute tree diversity properties. Canopy shadows embody forest canopy structure that is part of alpha diversity patterns. To obtain a better understanding of canopy shadows that may inform about forest dynamics, the extractions of canopy shadows was conducted in 18 aerial photomosaics (2 X 2 km each) of the Yutsuntsa and Sawastian communities using an object-based machine-learning classifier to extract canopy shadows in the aerial photographs. These photomosaics did not go through color balancing during the image mosaic processes, thereby showing variations in brightness and illumination throughout the images. To avoid bias during canopy shadow extractions due to these variations, trial and error of preprocessing was conducted aiming to minimize the variations and produce images with the most consistent colors and textures representing different features in the images. Convolution filtering, a process of averaging small sets of pixels across an image, showed the best performance. It aims to change the spatial frequency characteristics of an image, i.e. manipulating the number of changes in brightness value per unit distance for any particular part of an image (Jensen 1986). A new target pixel

value is based on the pixel values in a moving window (kernel) around the pixel of interest. An output data value for the central pixel being convolved derives from the following formula (Jensen 1986):

$$V = \left[\frac{\sum_{i=1}^{q} \left(\sum_{j=1}^{q} f_{ij} d_{ij} \right)}{F} \right]$$

where f_{ij} is the coefficient of a convolution kernel at position i,j (in the kernel), d_{ij} is the data value of the pixel that corresponds to f_{ij}, q equals the dimension of the assumed square kernel, F means either the sum of the coefficients of the kernel or 1 if the sum of coefficients is 0, and V is the output pixel value. The software Erdas Imagine 9.2 provided more than 30 filters in the convolution kernal library to choose from. After trying all the applicable filters I found that the 7 X 7 kernal with a summary filter offered the best preprocessing results for all the aerial photographs by minimizing the variations and producing images with the most consistent colors and textures representing different features in the images (Figure 3.3).

Figure 3.3. A comparison between aerial photomosaics before (left) and after (right) convolution filtering. The uneven brightness and illumination were significantly reduced after preprocessing.



A few previous studies mapped and characterized canopy gaps using remote sensing techniques. Foody et al. (2003) used maximum likelihood and fuzzy logic classifications to identify and estimate forest gap area, perimeter, and shape in fine spatial resolution multispectral imagery. Lundquist and Sommerfield (2002) employed Fourier transform and cluster analysis to map canopy gap distributions and characterize canopy gap size using aerial photographs. Plowes (2005) delineated canopy gaps in aerial photographs and then predicted the likelihood of canopy gap occurrences in Landsat TM images using subpixel analysis. With the increasing popularity of Light Detection And Ranging (LIDAR) in remote sensing, a forest pigment study used Compact Airborne

Spectrographic Imager (CASI) and LIDAR to mask out canopy gaps for a better characterization of canopy properties (Blackburn 2002). LIDAR has informed forest gap properties in terms of location, size, shape complexity, adjacent canopy height, and within- and inter-canopy relationship (Koukoulas and Blackburn 2004, Asner et al. 2008, Vepakomma et al. 2008). LIDAR also facilitated in examining tropical forest dynamics and disturbance regimes (Mueller et al. 2009a, 2009b). Traditional pixel-based classification methods were not applicable for my dissertation research, due to the lack of high-resolution multispectral imagery in the study area. Therefore, for mapping canopy shadows, I employed a classification method that has not been used previously in aerial photographs for studying forest gaps.

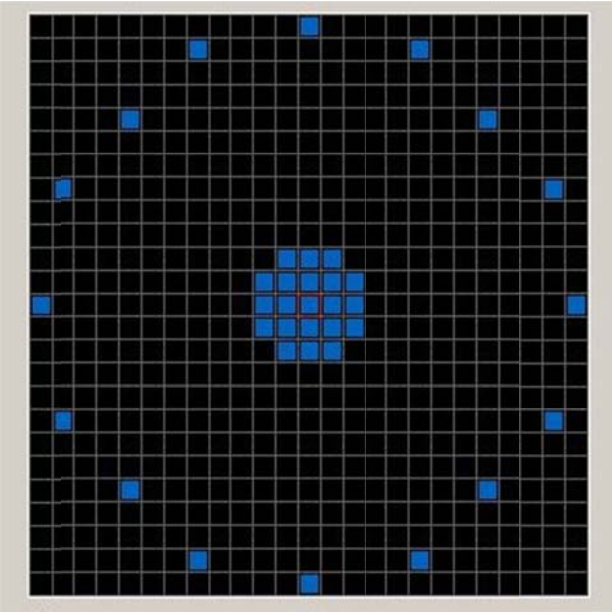
The analysis of aerial photomosaics employed object-based classification after extracting textural and color features from the image. Object-based classification delineates segments of real world objects and considers topological relations among neighboring pixels, thereby providing great details of canopies and differentiating tree crowns in high-resolution images (Bunting and Lucas 2006, Hájeck 2006). Differing from traditional pixel-based classifications, important parameters for object-based classification include spatial patch, grey level, color, and shape textures (Laliberte et al. 2004, Wang et al. 2004, Ivits et al. 2005, Ye et al. 2007). As an experiment, my dissertation research used the software Feature Analyst 4.2 (Overwatch Systems, Ltd.) for automated feature extraction to identify and locate canopy shadows. Feature Analyst used in Erdas Imagine requires a series of data training and processing steps. I first manually delineated at least 85 haphazardly selected canopy shadows in various sizes, textures, and shapes in each photomosaic as training samples. The canopy shadows here represented dark canopy openings resulting from topography relief, tree fall gaps, or natural forest

canopy openings. These hand-digitized input samples were stored as polygon shapes in a single-class GIS layer.

The preprocessed aerial photomosaics were rescaled into a 6-inch resolution, the smallest pixel size supported by Feature Analyst and recommended by Feature Analyst technical support. I employed the following analytical criteria within the Feature Analyst Set Up Learning environment: 1) determine the feature type as "natural features", 2) use all three bands (red, green, and blue) as band type of "reflectance", 3) apply the default histogram stretch, 4) use a specified input representation pattern (Figure 3.4), 4) aggregate the result polygons to a minimum object size of a specific number of pixels, and 5) smooth output shapes with a threshold of one pixel. Selecting the type and parameter of the input representation depended on trial and error for the best performance. Input representation allows a particular pattern algorithm to examine image pixels within a spatial pattern adjacent to the pixel of interest as well as other pixels to be considered during the classification (Miller et al. 2009). Input representation determines the shape and size of the input pixels through which Feature Analyst gathers spatial and spectral information for each pixel. It is used to classify each pixel in the image to examine if it is part of the target feature. Feature Analyst positions the center cell of the input representation pattern over each training pixel and records the spectral and spatial information associated with the pixel. It then creates a learning profile that defines the characteristics of the target feature. Feature Analyst positions the center cell of the input representation pattern over each pixel in the entire image and uses the learning profile to search for pixels similar to the training pixels (Visual Learning Systems 2009). The Bull's Eye 3 pattern, often used for extracting natural features such as trees and shrubs, appeared to be the most ideal input representation (Figure 3.4). The pattern width varied

among images, but at least covered the training samples and surrounding cells that did not belong to the samples.

Figure 3.4. Feature Analyst Bull's Eye 3 input representation at pattern width = 25. The central pixel = pixel of interest, other blue pixels = pixels to be considered during classification.



Post-classification pixel aggregation combined objects created after classification that comprised less than a particular number of pixels into neighboring objects. The aggregation pixel number varied among images, depending on the best extraction performance. The preliminary extraction resulted in very long processing time and a very large output shapefile. Therefore, I applied the smoothing process during classification to lower the computational effort by reducing vertices between feature class boundaries. Feature Analyst Technical Support recommended the smoothing threshold of one pixel.

A few important post-classification processes were conducted to improve the classification algorithm and to refine the output. I haphazardly visualized and selected correctly and incorrectly classified features (at least 200 for each type per image) as training examples and then reclassified the image using Feature Analyst's Clutter Removal function (Figure 3.5). The clutter-removed classification produced a more precise but underclassified product, thereby requiring another step of adding missed features during the classification. After manually delineating more canopy shadows that were not extracted during the clutter removal classification, I reran the feature extraction based on added missing features and the previous extraction. I repeated the clutter-removal and adding missed feature processes for several times until the classification presented a satisfactory result to minimize errors of omission, i.e. incorrectly excluding pixels from canopy shadows, or errors of commission, i.e. incorrectly assigning pixels to canopy shadows (Congalton and Green 2008) (Figure 3.6). To connect adjacent small canopy shadow polygons, I applied a dilate morphology filter that buffered pixel regions by the width of one pixel.

Figure 3.5. An example of Feature Analyst Clutter Removal. The red polygons represent features that were correctly identified whereas the yellow polygons represent the incorrectly identified features.

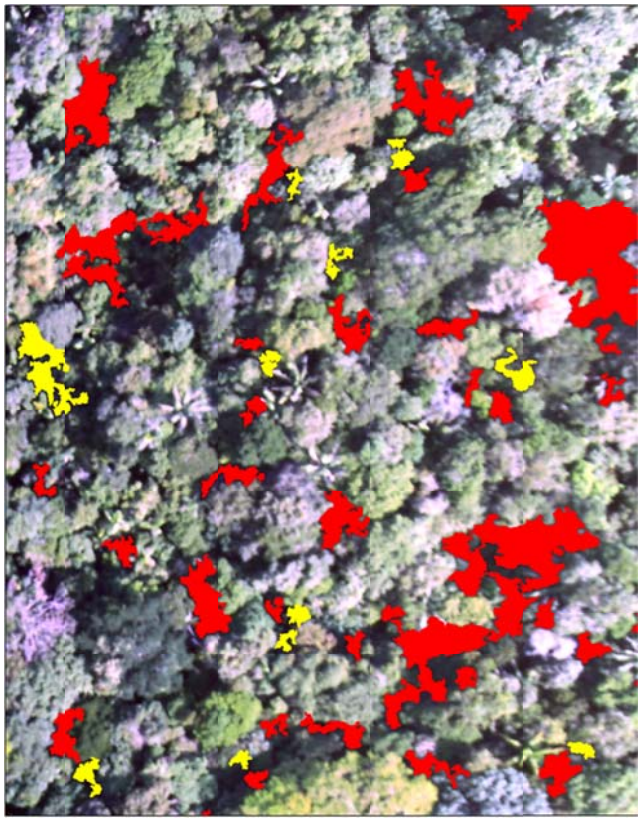
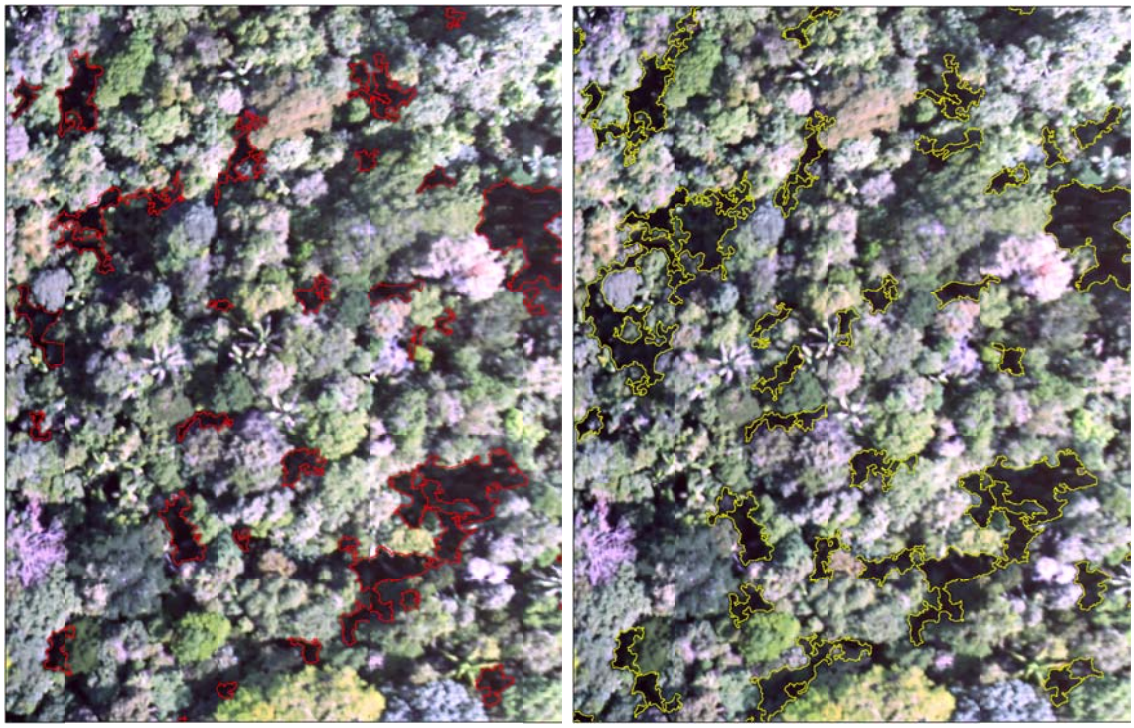


Figure 3.6. Canopy shadow extractions during different repeats of clutter removal and adding missed features. The red polygons represent the classification that slightly underestimated the feature class, whereas the yellow polygons show a slight overestimate of dark canopy openings.



Validating the classification results through accuracy assessment informs about the quality of the classification and has become an inherent component in remote sensing mapping projects (Grenier et al. 2008). Object-based classification differs from traditional pixel-based classifications by extracting spatial objects of relatively homogenous segments. Hence, accuracy assessment of object-based classification must ensure that the thematic accuracy is based on the object (Tiede et al. 2006). An extracted canopy shadow may encompass mixed pixels of varying colors and textures, thereby yielding different levels of canopy shadowiness. To consider this uncertainty introduced

by mixed pixels, a fuzzy logic approach may be the appropriate approach one for accuracy assessment (Fritz and See 2005). The fuzzy expression consists of several conditions that define the feature as typical, less typical, or atypical of a class. These conditions are often described as a degree of probability (Rahman and Saha 2008).

Accuracy assessment is necessary for evaluating classification products. I evaluated the canopy shadow extraction with a standard error matrix method (Congalton 2004). I constructed the error matrix using both traditional pixel-based sampling and object-based sampling under a binary (canopy shadow vs. non-shadow) classification scheme. The object-based sampling used the classification output polygon as the validation unit because it corresponded to a single canopy shadow (Mathieu et al. 2007). Error matrix describes classification accuracy and characterizes errors by providing measures of overall accuracy and accuracies of correct class allocation (Gao and Mas 2008). Overall accuracy indicates the likelihood of any category being correctly classified. User's accuracy reflects the probability of a pixel in the classified category representing that category on the ground, and producer's accuracy reveals how well a particular class is correctly classified on the map (Congalton and Green 2008, Vanderzanden et al. 2002).

In addition, I computed a K_{hat} value in KAPPA analysis to evaluate the level of agreement between the classified and reference data. An overall K_{hat} for the entire error matrix and conditional K_{hat} for individual classes (shadow and non-shadow) were calculated (Congalton and Green 2008). Z statistics was used to determine how much better the classification was compared to a layer where class value was randomly assigned to each pixel (Congalton 1991, Mathieu et al. 2007, Rahman and Saha 2008). An additional pairwise Z value was computed to determine whether the pixel-based and

the object-based sampling methods showed significant differences (Congalton and Green 2008).

Congalton (1991) and Congalton and Green (2008) suggested the use of a rule to collect a minimum of 50 samples for each classification class. Nevertheless, considering the massive number of extracted polygons in each image, 50 samples appeared to be insufficient. Congalton and Green (2008) suggested another computation of sampling size N based on a multinomial distribution:

$N = B\Pi i(1-\Pi i)/bi^2$

B is the upper tail of the chi square distribution with one degree of freedom (X^2 (1, 0.975) = 5.02), Πi is the proportion of the i^{th} class (here accordingly to the canopy shadow class) in the map area, and b is the desired precision (5%). As the result, the total samples for assessing each classification ranged from 72-149 among the 18 images. To ensure that there would be sufficient samples for both canopy shadow and non-shadows classes, I doubled the above sample size to collect 72-149 samples within each respective class of canopy shadow vs. non-shadow.

For the pixel-based assessment method, I conducted stratified random sampling using Sampling Design Tools (Center for Coastal Monitoring and Assessment, 2007) (http://ccma.nos.noaa.gov/products/biogeography/sampling/welcome.html) for ArcGIS and the Create Random Points Tool in ArcGIS 9.3 to generate spatially stratified random points in each image (Jensen 2004, Congalton and Green 2008, Gao and Mas 2008, Zhou et al. 2008). The binary error matrix was derived from visualizing whether or not the random point that fell inside or outside a classification polygon belonged to a real canopy shadow visualized in the image.

For the object-based assessment method, the sampling objects that were within the canopy shadow class were created by selecting classified polygons with a probability

proportional to their area using Hawth's Tools for ArcGIS (Beyer 2004, http://www.spatialecology.com/htools). Radoux et al. (2008) proposed this selection method in order to account for the fact that misclassifying a large object had greater impact on the overall accuracy than misclassifying a small object. The binary error matrix was derived from visualizing whether or not > 50% area of the selected polygon overlapped with a real canopy shadow visualized in the image, or if the polygon covered < 50% area of a canopy shadow. I also selected spatially stratified random 10 X 10 m vector grids that were in the non-shadow class and visualized whether or not the grid overlapped with a real canopy shadow for at least the minimum area of a classified polygon selected by the above weighed sampling.

In addition, I selected spatially stratified random classified polygons (unweighed) and categorized the selected polygons into a fuzzy agreement in their proportion coverage of real canopy shadows from the image into >75%, 50-75%, 25-50%, and < 25% area of the real canopy shadows. This categorization summarized the level of agreement between canopy shadow extraction and the aerial photograph.

Spatial patterns of canopy shadows

To examine the spatial characteristics of the extracted canopy shadows, I computed a series of landscape metrics in area, patch density and size, edge, and shape (Hernandez-Stefanoni 2005, 2006). The computation was conducted using the Patch Grid extension of Patch Analyst 4 for ArcGIS (Spatial Ecology Program, Centre for Northern Forest Ecosystem Research, Lakehead University). The metrics included total area, number of patches, patch density at the landscape, mean patch size, mean patch edge, landscape shape index, area-weighed mean shape index, mean nearest neighbor, and mean proximity index (McGarigal and Marks 1994 and 1995, Ritters et al. 1995).

The spatial characteristics of the size of canopy shadows, in particular patterns of global and local spatial autocorrelation, were examined by computing global and local Moran's I and Getis-Ord General G indices using ArcGIS 9.3 and OpenGeoDa (GeoDa Center for Geospatial Analysis and Computation, Arizona State University). Moran's I and the General G are recommended to be used in conjunction with each other to allow deeper understanding of spatial variation that can be compared and contrasted (Getis and Ord 1992). Moran's I (Moran 1950) measures global spatial autocorrelation to detect spatial patterns departing from randomness. Positive Moran's I indicates that nearby areas have similar values and impose global spatial clustering. In addition, I aimed to elucidate patterns of local spatial autocorrelations of canopy shadow properties. While global Moran's I describes an overall spatial pattern in the study region, Local Spatial Autocorrelation (LISA) using Anselin's local Moran's I (Anselin 1995) detects local spatial autocorrelation by identifying local clusters (regions where adjacent areas have similar values) or spatial outliers (areas distinct from their neighbors in terms of the values):

$$I_i = \frac{(y_i - \bar{y}) \sum_{j=1}^{n} w_{ij} (y_j - \bar{y})^2}{m_2}$$

Where m_2 is the average of the squared deviations from the mean:

$$m_2 = \frac{\sum_{j=1}^{n} (y_j - \bar{y})^2}{n}$$

LISA decomposes Moran's I into contributions for each location in the study region. The sum of local Moran's I for all observations is proportional to global Moran's I (Anselin 1995). By linking directly to global spatial autocorrelation, LISA enables assessment of influential spatial clusters or outliers by gaining insight into aspects of different spatial regimes in the degree of spatial association types (Anselin 1993, 1995).

The General G measures how concentrated the high or low values are for a given study region:

$$G = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} w_{i,j}x_i x_j}{\sum_{i=1}^{n}\sum_{j=1}^{n} x_i x_j}, \ \forall j \neq i$$

Where x_i and x_j are values of features i and j and $w_{i,j}$ is the spatial weight (Getis and Ord 1992, ArcGIS Desktop Help). The Z score associated with the General G represents the intensity of the spatial clustering. Positive Z score indicates clustering of high values (Getis and Ord 1992).

Palm distribution patterns

The tree beta diversity study in western Amazon focused on the macro-scale heterogeneity of species diversity and distribution in association with biogeographic boundaries and climatic factors. The extent to which individual species differ spatially in their way of occurrence at the landscape is also critical for characterizing beta diversity. Due to the limitation in data availability and analysis effort for multiple species, I only examined landscape-level characteristics of particular canopy tree species. Palms represent a unique taxonomic group in the Neotropics and are often important members of forest communities. With an interest in obtaining distribution information in the study area for future beta diversity studies, three canopy palm species of *Mauritia flexuosa, Socratea exorrhiza,* and *Oenocarpus bataua* that have distinctive crown characteristics and are discernible directly from above the canopy were studied. I visualized, located, and identified all individuals of these three species in 52 mosaicked aerial photographs (at a 5-cm resolution) across four flight lines in the study area (Figure 3.2, 3.7). These mosaicked aerial photographs were products of still images that were derived from R.

Sierra's digital video acquisition in 2006 (see above). Computations of the abundance, density (number of individuals/ha), average distance to the nearest conspecific neighbor, minimum distance to a conspecific neighbor, and multi-distance spatial cluster analysis were conducted in ArcGIS 9.3 (ESRI, Inc.). Multi-distance spatial cluster analysis is based on Ripley's K-function as a way to analyze spatial pattern of point data by summarizing spatial dependence (clustering or dispersion) over a range of distances (Getis 1984, Boots and Getis 1988).

Figure 3.7. *Mauritia flexuosa* (in yellow circle), *Socratea exorrhiza* (in blue circle), and *Oenocarpus bataua* (in red circle) in the aerial photographs at 5-cm resolution.

Landscape zonation map design in the Ecuadorian Amazon

Landscape scale land cover classification and accuracy assessment

The first two parts of this dissertation examined alpha and beta diversity properties and patterns respectively at the plot- and region-based scale. Alpha and beta diversity features, such as gradients and heterogeneity driven by habitat- or distance-related factors, are harbored within various types of land cover. Characterizing landscape covers initiates a broad-scale understanding of what constitutes biodiversity from a top-down perspective. Furthermore, biodiversity conservation planning often uses land cover types as references to indicate fragile or threatened habitats. Moving from understanding biodiversity patterns to the applied aspects in conservation biogeography, I aimed to create a new habitat/vegetation map of the study area that can serve as a references for future coarse-scale regional diversity and conservation research. A land cover classification was conducted using four Landsat ETM+ images of the study region from September, October, and November 2002 with an object-based machine-learning classifier. Like the canopy shadow extractions study (see above), the parameterization, machine learning, and feature extractions were based on trial and error. Systematic factors such as earth rotation and non-systematic factors such as altitude variance can affect the geometric quality of an image (Jensen, 2005). I did not perform geometric corrections for the ETM+ images due to the lack of reference images in which the image displacement caused by terrain relief and camera tilt has been removed (Jensen 2007). However, using these images for land cover classification was acceptable considering all four Level 1T ETM+ images provided systematic radiometric and geometric accuracies by incorporating ground control points while employing a Digital Elevation Model (DEM) for topographic accuracy (USGS documentation).

Image pan-sharpening was done to merge the low-resolution multispectral bands with the high-resolution panchromatic band by resampling to the pixel size of the panchromatic band (15 m). Pan-sharpening involves fusing higher-resolution panchromatic raster band with a lower-resolution multi-band raster set. It produces a multi-band raster with the resolution of the panchromatic band (Jensen 2004). Object-based classification required a decent amount of data training samples that were delineated to cover heterogeneous colors, textures, and patterns of each land cover class. A series of preliminary trial and error revealed that it was not feasible to obtain good data training samples that would result in satisfactory classification products to distinguish different land cover types in the region at a 30-m spatial resolution of the multispectral bands of ETM+ images. Hence, I applied the Gram-Schmidt spectral sharpening method with ENVI 4.5 (ITT Visual Information Solutions, Inc.) to first simulate a panchromatic band from the multispectral bands. The Gram-Schmidt algorithm then transformed the simulated panchromatic band and the multispectral bands using the simulated panchromatic band as the first band. A swapping of the original panchromatic band with the first Gram-Schmidt band occurred, followed by the inverse Gram-Schmidt transform to form six pan-sharpened multispectral bands at a 15-m spatial resolution (ENVI Help).

Atmospheric correction was necessary for reducing the atmospheric influence on water-leaving light signals (Jensen 2007). A dark pixel subtraction was conducted because it did not require atmospheric and meteorological data in comparison to other more sophisticated techniques. The dark pixel subtraction is based on the assumption that an effective black body exists in the image and by removing the minimal pixel values for each band the effect of atmospheric conditions are adjusted (Hadjimitsis et al. 2004). Dark pixel subtraction searches each multispectral band for the darkest pixel value because this method assumes that dark objects do not reflect lights, and therefore any

pixel value greater than zero must result from atmospheric scattering. The scattering is removed by subtracting this value from every pixel in each band (ENVI Help).

The radiance observed by a remote sensor is affected by bidirectional effects that are governed by the illumination conditions, the viewing geometry, and the atmospheric conditions. I evaluated a local radiometric correction method that employs one image that is less affected by the bidirectional reflectance for the local adjustment of the pixel values of the targeted image (Tuominen and Pekkarinen 2004). However, the preliminary results indicated that this illumination correction method did not result in visually discernible changes in the images.

As an experiment, my dissertation research used the software Feature Analyst 4.2 (Visual Learning Systems, Inc.) for automated feature extraction to classify habitat and vegetation types from these pan-sharpened ETM+ images. Pixel-based classification of land cover was conducted in the study area (Lopez 2008), but object-based imagery analysis has never been done. Feature Analyst used in Erdas Imagine requires a series of data training and processing steps. These hand-digitized input samples were stored as polygon shapes in a single-class GIS layer.

Lopez (2008) conducted a preliminary unsupervised classification of the Achuar and Shiwiar territories and divided the vegetation and land cover into nine classes: human land use, lowland evergreen forest on flat terrain, lowland evergreen forest in floodable white water, lowland evergreen forest on hilly terrain, palm swamp, secondary vegetation, shrub and grass vegetation, upper lowland evergreen forest on hilly terrain, and water. Initial visual inspections revealed that Lopez's classification scheme, with an additional class of cloud cover, offered distinguishability in terms of texture, colors, and patterns for the habitat types among the four pan-sharpened ETM+ images. For each image, I created at least 25 training sample polygons for each of the ten classes before

merging all training samples into a multiclass training file. Four training files with over 1,000 sample polygons were created.

The following analysis criteria were used within the Feature Analyst Set Up Learning environment: 1) determine the feature type as "land cover features", 2) use all six bands as band type of "reflectance", 3) apply the default histogram stretch, 4) use the Bull's Eye 3 pattern as the input representation, 4) aggregate the result polygons to a minimum object size of a specific number of pixels, 5) smooth output shapes with a threshold of one meter, and 6) wall-to-wall classification to classify every pixel in each image. The input representation pattern width varied among images, but at least covered the training samples and surrounding cells that did not belong to the samples. The post-classification aggregation pixel number also varied among images, depending on the best extraction performances. Finally, I haphazardly visualized and selected a number of correctly and incorrectly classified features as training examples and then reclassified the images using Feature Analyst's Clutter Removal function.

The three-band ASTER images served as the reference data for the accuracy assessment of the classifications. Traditionally the reference data of accuracy assessment have a higher spatial resolution for enhancing the visual comparisons between the classified land cover types and the reference image (Jensen 2007). However, due to the unavailability of other georeferenced images in the study region, the six ASTER images at a 15-m spatial resolution were the best options for accuracy assessment. The ASTER images worked well for the visual inspections of accuracy assessment, but a preliminary land cover classification using these ASTER images did not perform correctly because several unique vegetation types could not be separated. What contributed to the low classification performance using ASTER might be that the three multispectral bands did

not capture sufficient spectral, textural, and chromatic variation among different vegetation types.

Like the accuracy assessment for canopy shadow extractions (see above), I established pixel-based and object-based error matrices for evaluating the land cover classifications. Each error matrix described the overall accuracy, user's accuracy, and producer's accuracy (see above) (Congalton and Green 2008, Vanderzanden et al. 2002). I then computed a K_{hat} value in KAPPA analysis to evaluate the level of agreement between the classified and reference data. An overall K_{hat} for the entire error matrix and conditional K_{hat} for individual classes were calculated (Congalton and Green 2008). Z statistics was used to determine how much better the classification was compared to a layer where class value was randomly assigned to each pixel (Congalton 1991, Mathieu et al. 2007, Rahman and Saha 2008). An additional pairwise Z value was computed to determine whether the pixel-based and the object-based sampling methods showed significant differences (Congalton and Green 2008).

Accuracy assessment of the classification was only conducted within this dissertation's focal study area in the Ecuadorian Amazon. The accuracy assessment of canopy shadow extractions (see above) computed the sampling size based on a multinomial distribution recommended by Congalton and Green (2008). Nevertheless, given that the proportion of map area among different land cover classes differed greatly, this sampling size calculation would result in a wide range of sampling size from less than 10 to a few hundred. Congalton (1991) and Congalton and Green (2008) suggested the use of a rule to collect a minimum of 50 samples for each classification class. I collected 55 samples for each class for each error matrix, with total 990 samples for two matrices. For four EIM+ images, I collected 3,960 samples. These samples were collected individually from image-based classification results, merged into single point (for pixel-

based sampling) and polygon (for object-based sampling) shapefiles, and then used for accuracy assessment.

For the pixel-based assessment, I conducted a stratified random sampling using the Generate Random Points function in Hawth's Tools for ArcGIS (Beyer 2004) to generate spatially stratified random points for each land cover class (Jensen 2004, Congalton and Green 2008, Gao and Mas 2008, Zhou et al. 2008). The error matrix was derived from visualizing whether or not the random point that fell inside a classified polygon of a particular class (input data) belonged to the corresponding class visualized in the reference ASTER images (reference data). In the error matrix, I documented the number of samples chosen from the class of an input data that fell into individual classes in the reference data.

For the object-based assessment, the sampling objects that were within each land cover were created by using the Stratified Random function in Sampling Design Tool for ArcGIS (Center for Coastal Monitoring and Assessment, 2007) (see above). The error matrix was derived from visualizing whether or not > 50% area of the selected polygon of a given land cover class overlapped with the corresponding class visualized in the ASTER images, or if the polygon covered > 50% area of a different land cover class. In each error matrix, I documented the number of samples chosen from the class of an input data that fell into individual classes in the reference data.

Zonation map design using land cover classification and other spatial data

Ultimately, conservation biogeography seeks to link biodiversity science into real-world conservation planning. Traditional conservation planning employs gap analysis that overlays data layers of species distribution, land cover types, and status of stewardship to identify "gaps" for conservation (e.g. Brooks et al. 2004, Rodrigues et al.

2004a, b, Martinuzzi et al. 2008, 2009). Species distribution can be mapped using habitat suitability modeling based on sampled species occurrences and environmental layers that may represent gradients of species habitat suitability (e.g. Buermann et al. 2008, Saatchi et al. 2008, 2009). However, in the Ecuadorian Amazon where species distribution data are scarce and spotty, species occurrence data only represent small-scale sampling efforts in inventory plots or along transects (e.g. EcoCiencia, unpublished reports). It is necessary to employ a method that does not require species distribution or habitat suitability maps, and yet still incorporates landscape features that represent the degree of importance with respect to biodiversity.

Previous studies indicated that the indigenous communities rarely utilize wetlands, seasonally flooded forests, palm swamps, and riparian forests (S. Lopez and R. Sierra, personal communications). These habitats harbor a great variety of tree communities and may potentially become important sites for conservation. The habitat classes based on the object-based habitat classification of the ETM+ images may provide some aspects of the vegetation information in order to facilitate the decision making of designing landscape zonation maps. Furthermore, spotting areas with great habitat heterogeneity and species diversity in the study region also contributed to the determination of biodiversity conservation sites. I conducted pattern metrics analysis after the image classification to attain details concerning habitat characteristics and diversity. The map showing areas with great habitat heterogeneity provided ancillary information for future conservation projects.

An a priori understanding of land cover and distribution patterns of landscape features facilitates the design of a zonation map that represents the degree of importance of the landscape regarding biodiversity. Due to the lack of sufficient biota information in the study area, for this dissertation research I could not create zonation maps that are

biologically meaningful. Instead, the zonation maps only showed site selections based on my interpretations of the importance of different landscape features for future conservation work. Areas known for harboring greater species diversity should receive higher preferences of inclusion inside the zonation map. In order to avoid conflicts with local interests, areas with residences and local land use may be excluded unless the objective of conservation explicitly includes preserving indigenous culture and land use upon a request made by the local people. In the following section I explain how I developed assumptions for this chapter's analysis. Due to the limitation in budget, time, and the logistics, my assumptions were derived from field observations and interpretations, not from formal studies or interviews. Therefore, this exploratory analysis inherited certain levels of bias.

The software ConsNet (Ciarleglio 2008, Ciarleglio et al. 2009, 2010) was used for designing zonation maps in the Achuar, Shiwiar, and Zapara territories in the Ecuadorian Amazon using remote sensing and GIS information, as well as criteria for spatial arrangement. ConsNet aims to minimize the area of selected land that is sufficient to contain and protect a specified representation of biodiversity whilst simultaneously optimizing a variety of costs and spatial criteria such as size, compactness, replication, connectivity and alignment (de Pous et al. 2011). ConsNet is also capable of integrating a variety of spatial criteria such as size, compactness, connectivity, replication, and alignment. In addition, users can introduce other criteria, such as socio-economic factors that affect the creation and decision of zonation maps (Ciarleglio 2008, Ciarleglio et al. 2009, 2010). ConsNet is built on the Modular Abstract Self-Learning Tabu Search (MASTS) framework, a metaheuristic algorithm that relies on memory structures to organize and navigate the search space (Ciarleglio et al. 2009, 2010). The self-learning tabu search avoids revisiting solutions that were discovered in previous iterations of

search (Ciarleglio 2008). Tabu search supports objectives based on preset rules and neighborhood selections that control the spatial arrangement of the network structure (Ciarleglio et al. 2009, 2010). These techniques can improve search performance and efficiency by directing the search to promising regions and reducing the number of evaluations (Ciarleglio 2008). During the processes of selecting raster grid cells to be included in the zonation map, ConsNet makes a binary decision and orders grid cells hierarchically based on its value for biodiversity conservation.

Previous studies used models of species habitat suitability as biodiversity surrogates to create conservation area networks using ConsNet (e.g. Illoldi-Rangel et al. 2008, Sarkar et al. 2009, Urbina-Cardona and Flores-Villela 2010, de Pous et al. 2011). In regions that do not have information of habitat suitability, datasets that consist of environmental and physical features can serve as surrogates for biodiversity (Sarkar et al. 2007, Sarkar and Illodi-Rangel 2010). Due to the lack of species occurrence information across the study area, habitat suitability modeling could not be carried out. Furthermore, the lack of sufficient species occurrence information made it difficult to obtain status of conservation for endangered, threatened, or sensitive species. Therefore, designing conservation area networks was not applicable during this stage of analysis. Instead, habitat classifications, remote sensing, and GIS data were used to create zonation maps with arbitrary targets. Because arbitrary targets did not contain biological meanings, the zonation maps only represented the degree of importance of the landscape based on my interpretations and my best knowledge of the study area.

For creating a zonation map in the Ecuadorian Amazon, I employed and compared a biodiversity- vs. a people-oriented approach. The biodiversity-oriented approach aimed to set primary preferences in areas that potentially harbor greater biodiversity without interfering with the existing land use. On the other hand, the people-

oriented approach prioritized in choosing areas that had the lowest likelihood to be utilized by the indigenous communities. Both approaches used identical sets of environmental layers for land feature characterizations, including classified habitat types using object-based classification method (see above), elevation and slope from digital elevation model, and GIS data of large rivers, small rivers, major drainage basins, and soil types (GIS data obtained from S. Lopez, R. Sierra, and M. Montoya).

More specifically, I excluded areas of existing human land use from the analysis in both approaches. The exclusion, however, did not imply that indigenous communities would be displaced. In fact, my conversations with the local people in summer 2008 and with other field researchers who have worked in the same study area between 2008 and 2010 revealed that expressions of hostility and doubts towards the practicality of ecological and conservation studies began to rise (S. Lopez and staff from EcoCíencia, personal communications). Researchers, including myself, have been told that the communities do not want their residential and existing land use areas to be interfered with any potential adjustment based on technical recommendations made by researchers or NGOs. Thus, for creating landscape zonation maps at this stage, I chose to exclude areas containing communities and current land use. The dynamics of local opinions and needs may change at any time and therefore, whether or not and how areas of indigenous residence and land use are included in future conservation planning remain as ongoing and open discussions.

Based on my field observations and a previous study by Lopez (2008), the indigenous communities intensively utilize areas within about 2 km around the village centers and flight paths, and within about 100 m around trails between villages (Illustration 3.6A, 3.6B, 3.6C, 3.6D). Areas at lower elevation and flatter slope, as well as riparian zones are likely to harbor great diversity of flora and fauna (EcoCíencia,

unpublished data), but are also areas where villagers cultivate, hunt, and fish. In particular, riparian zones within 200 m from large rivers and 100 m from small rivers have been included in the conservation area network of a previous study in the Merauke region, Indonesia (Sarkar et al. unpublished data). Areas classified as human land use based on the object-based Landsat ETM+ image classification were also excluded. In western Amazon, indigenous people produce to satisfy their demands for food (Lopez and Sierra 2010). Descola (1987) and Taylor (1999) believed that cultural factors played some role in agricultural patterns, but Lopez and Sierra (2010) found that these factors appear to be less important than what was previously valued.

Illustration 3.6. Residential center (A), area for waterways (B), result of hunting (C), and palm oil extraction (D) in the indigenous communities.

A.

B.

C.

D.

The relative preferences among different classes of each land feature type differed between the biodiversity- vs. people-oriented approaches (Table 3.2). For the biodiversity-oriented approach, preferences were given to the classes of elevation, slope, river, drainage basin, habitat, and soil that are likely to harbor greater diversity of the flora and fauna. The preferences for the people-oriented approach were assigned to the classes that are less likely to be affected by indigenous land use. For example, I assigned lowland evergreen forest on mixed terrain, lowland evergreen forest on flat terrain, palm swamps, and secondary forests higher weights of preferences for the biodiversity-oriented approach because a previous report documented greater fauna diversity in these habitats (EcoCíencia, unpublished data). On the other hand, lowland evergreen forest on mixed terrain and palm swamps had higher weights than other habitats for the people-oriented approach because these two habitats are least visited and utilized by the indigenous communities (Lopez 2008). Similarly, soil types K8, K4, and K12 (Figure 2.11 in Chapter 2: Study Area for soil identifications) had greater weights compared to other soil types because these soils with lower fertility are less likely served for farming and cultivation. The distribution of these weights and preferences inherited my knowledge and interpretations and therefore, the analysis was carried out with some bias.

Table 3.2. Relative weights (in percentage) of each landscape feature compared to other features of the same type. The weights were used for determining targets of land features that needed to be met under the total 10%, 20%, 30%, and 40% targets. See soil identifications in Figure 2.11.

Land feature type	Biodiversity	People
Flight path inside 2 km buffer	Excluded	
Human land use	Excluded	
Trail inside 100 m buffer	Excluded	
Village inside 2 km buffer	Excluded	
Elevation 158-338 m	35	30
Elevation 338-518 m	35	35
Elevation 518-697 m	30	35
Slope 0-12 degrees	35	30
Slope 12-24 degrees	35	35
Slope 24-36 degrees	30	35
Large river inside 200 m buffer	55	55
Large river outside 200 m buffer	45	45
Small river inside 100 m buffer	55	55
Small river outside 100 m buffer	45	45
Tigre basin	30	25
Pastaza basin	30	25
Morona basin	25	25
Napo basin	15	25
Cloud	0	0
Water	0	0
Lowland evergreen forest on mixed terrain	15	15
Lowland evergreen forest on flat terrain	20	12
Lowland evergreen forest on hilly terrain	10	12
Lowland evergreen forest in white water	10	12
Palm swamp	15	20
Secondary forest	15	5
Shrub and grass vegetation	5	12
Upper lowland forest on hilly terrain	10	12
Soil type H1	4.6	4
Soil type F1	4.6	4
Soil type K8	3	6.67

(Table 3.2 continued)

Soil type E9	4.6	4
Soil type N4	4.6	4
Soil type K7	4.6	4
Soil type K2	4.6	4
Soil type K9	4.6	4
Soil type H2	4.6	4
Soil type F2	4.6	4
Soil type Inceptisol Tropept	4.6	4
Soil type K	4.6	4
Soil type Inceptisol Andept	4.6	4
Soil type Entisol Fluvent	4.6	4
Soil type Inceptisol Aquept	4.6	4
Soil type K3	4.6	4
Soil type Entisol Orthent	4.6	4
Soil type H3	4.6	4
Soil type K1	4.6	4
Soil type Histosol Fibrist	4.6	4
Soil type K6	4.6	4
Soil type K4	3	6.67
Soil type K12	3	6.67

The ConsNet search was conducted using grid cells at a spatial resolution of 120 m across 930,788 cells for approximately 13,403 km^2 in the study area (i.e. 1,053,886 cells of the study area minus 123,098 cells excluded from the analysis). This spatial resolution was determined based on a previous conservation area network design that used a resolution of 100 m (Sarkar et al. unpublished data). I employed searches with goals to minimize areas and optimize shapes of the zonation map. To reduce computational time and effort, the approach to optimize shape compactness, rather than to minimize number of clusters, was selected. A few other factors were also considered regarding choosing the shape optimization approach. First, to obtain the best shape score in ConsNet, the shape optimization approach facilitated in increasing spatial connectivity

to link large areas (M. Ciarleglio, personal communication). Second, the cluster minimization approach was based on the idea that a study region is threatened by disturbances and future development (M. Ciarleglio, personal communication). Currently the land in southeastern Ecuador is not under immediate threat. This region is different from Yasuní National Park in northeastern Ecuador, where pressing threats from petroleum and road construction persist (Bass et al. 2010). Even if certain selected areas in the zonation maps are disconnected from other selected areas, they are unlikely to face significant threats because the surrounding areas are still likely undisturbed (M. Ciarleglio, personal communication).

Therefore, the searches only employed criteria regarding shape and distances to land use and rivers (Table 3.3). Both biodiversity- and people-oriented approaches aimed to minimize ConsNet's shape score in order to optimize shape compactness. To reduce impact on current and future indigenous land use, both approaches sought to maximize average distances from the selected areas to the nearest community center, flight path, and trail (Table 3.3). The biodiversity-oriented approach aimed to minimize average distances between the selected areas and rivers because the riparian ecosystem is likely to harbor great species diversity, especially the aquatic fauna. In contrast, the people-oriented approach sought to maximize average distances to rivers, which are frequently used for fishing and local transportation (Table 3.3).

Table 3.3. List of criteria used in the minimum area searches for the biodiversity- and people-oriented approaches. The weights (sum = 1) represent the relative importance of the criteria.

	Treatment		Weight	
Measure	Biodiversity	People	Biodiversity	People
Shape	minimize	minimize	0.5	0.45
Distance to the nearest community	maximize	maximize	0.125	0.15
Distance to the nearest flight path	maximize	maximize	0.125	0.15
Distance to the nearest trail	maximize	maximize	0.125	0.15
Distance to the nearest large river	minimize	maximize	0.0625	0.05
Distance to the nearest small river	minimize	maximize	0.0625	0.05

Eight scenarios were created based on two approaches (biodiversity- and people-oriented); each approach was defined by four sets of arbitrary target values of 10%, 20%, 30%, and 40%. A target of representation for a biodiversity surrogate is defined as the amount of the surrogate that must be present within the units of the zonation map (Margules and Sarkar 2007). The World Wildlife Fund and IUCN (Dudley et al. 1996) have advocated a target of 10% for all forest types on Earth. Other previous studies set targets of representation from 5%-40% (e.g. Illoldi-Rangel et al. 2008, Sarkar et al. 2009, Urbina-Cardona and Flores-Villela 2010, Sarkar et al. unpublished data). Currently there are no policies or specific expectation from the indigenous territories in the Ecuadorian Amazon to indicate goals of conservation. In addition, the lack of species habitat

suitability (i.e. biodiversity surrogates) information and species conservation status in the study area made it impossible to determine targets of biodiversity representation. Because these targets were defined arbitrarily and were uniform (i.e. they did not vary accordingly to species conservation status), these targets with no biological meanings were only used for creating zonation maps, not for designing conservation area networks.

ConsNet requires an input target file to indicate the desired number of grid cells to be selected in each class of its corresponding land cover type. The relative weight of each land feature class indicated in Table 3.2 was used to calculate the desired target:

$$\text{Target number of cells} = \frac{\text{Total cells in study area} \times \text{Target}}{\text{Sum of (A in each land feature type)}}$$

$$\times(\text{A for a class in a land feature type})$$

$$\text{Whereas A} = \frac{\text{Total cells of a class in a land feature type} \times \text{Weight in Table 3.1}}{100}$$

For each scenario, it was necessary to establish a lower bound for the number of grid cells that was required to meet the targets (Table 3.4). This involved solving the basic set cover problem using the MDS-C objective, which only aimed to minimize the number of selected cells. The MDS2 adjacency heuristic algorithm was used because it provides the best solution based on selecting the fewest cells and generating the lowest shape score (Urbina-Cardona and Flores-Villela 2010). The MDS2 algorithm uses concepts similar to rarity and complementarity to select cells that are contiguous with cells that are selected in previous iterations (Ciarleglio et al. 2008, Urbina-Cardona and Flores-Villela 2010). A neighborhood selection called “escape with spatial neighborhood” was enabled to ensure that a compact zonation map would be created when adding or deleting grid cells in order to attain the best shape (Urbina-Cardona and

Flores-Villela 2010). A refinement search was then applied to obtain the final bound of minimum and maximum number of cells that were required to meet the targets (Table 3.4). In this step the neighborhood selection called "large neighborhood only" was applied by using large neighborhoods to thoroughly explore the space around the current solution (Urbina-Cardona and Flores-Villela 2010).

After obtaining the upper and lower bounds of the number of cells that were required to meet the targets from the previous searches, a minimum area objective was used to thoroughly search for the best solutions (Table 3.4). This search included the established criteria (Table 3.3) and a new constraint that required the number of selected cells to be no more than 2% above the upper bound. The "aggressive" neighborhood selection was enabled for meticulous spatial rearrangement moves for expanding or shrinking spatial clusters, removing or adding cells, smoothing shapes, and filling holes or voids (M. Ciarleglio, personal communication). The final step of the zonation map optimization began from the best solution from the previous objection function (Table 3.4). This refinement assessed a large number of possible moves and made improvements that might have been missed (Ciarleglio et al. 2009).

Table 3.4. Summary of processes and settings used in ConsNet.

Process	objective	Start location	Neighborhood selection	Maximum iterations
Establish a lower bound for the number of cells that will be required to meet the targets	MDS-C Minimize the number of cells	Best known heuristic solution (MDS2)	Standard	1,000,000
⬇				
Refinement search from the previous step	MDS-C Minimize the number of cells	Best known solution found from the previous step	Basic	10,000
⬇				
Multi-criteria minimum area search	MCA Multi-criteria minimum area	MDS2 adjacency	Aggressive	3,000,000
⬇				

(Table 3.4 continued)

Refinement search from the previous step	MCA Multi-criteria minimum area	Best known solution found from the previous step	Basic	10,000

Chapter 4: Alpha diversity and forest structure in the Ecuadorian Amazon

RESULTS

Species composition and diversity

In this chapter I describe the local, fine-scale alpha diversity patterns that are the first step for understanding biodiversity and species distribution for conservation biogeography research. The results described in this chapter are based on field work of tree inventories conducted in 2006 for alpha diversity studies.

The plot in Yutsuntsa had the greatest number of emergent and canopy trees whereas the plots in Juyuintsa and Sawastian had more understory trees. Although the plot in Sawastian had the lowest tree abundance, it showed the largest total basal area contributed by the emergent trees with large diameter in the plot (Table 4.1). The plot in Juyuintsa, with the highest tree abundance, also had the greatest number of genera and species. The five most abundant species accounted for 19.9%, 21.1%, and 31.5% of total number of individuals in Yutsuntsa, Juyuintsa, and Sawastian, respectively (Table 4.1). The plot in Yutsuntsa did not show much lower species diversity compared to the plot in Juyuintsa, but the plot in Sawastian showed 54-65%, 16-18%, and 64-69% lower diversity than the Yutsuntsa and Juyuintsa plots in Fisher's alpha, Shannon-Wiener, and Simpson's inverse diversity indices, respectively (Table 4.1). Dominant emergent trees in the Yutsuntsa plot comprised species of *Inga* (Mimosaceae) whereas the most dominant canopy trees consisted of species of *Eschweilera* (Lecythidaceae), *Inga*, *Virola* (Myristicaceae) and *Micropholis* (Sapotaceae). For the plot in Juyuintsa, *Iriartea deltoidea* (Arecaceae) and species of *Inga* as well as *Virola* were the dominant emergent trees. *Iriartea deltoidea* and species of *Ocotea* (Lauraceae) and *Sterculia* (Sterculiaceae)

were the most dominant canopy trees. *Terminalia oblonga* (Combretacaeae) and *Acacia glomerosa* (Mimosaceae) were the dominant emergent trees in Sawastian, whereas *Pachira punga-schunkei* (Bombacoideae within Malvaceae) and *Sapium marmieri* (Euphorbiaceae) were the most dominant canopy trees. All three plots had species from the Urticaceae or Cecropiaceae families (e.g. species of *Cecropia*, *Pourouma*, or *Urera*), which often establish after recent disturbance. The Sawastian plot had a higher percentage of individuals that belonged to Urticaceae or Cecropiaceae than plots in Yutsuntsa and Juyuintsa (Table 4.1).

Table 4.1. Tree abundance, basal area, number of families, genera, and species, and species diversity indices of the three 1-ha plots.

	Yutsuntsa	Juyuintsa	Sawastian
Total number of individuals	610	622	555
Emergent trees	41	44	23
Canopy trees	145	103	56
Subcanopy trees	134	108	127
Understory trees	290	367	349
Total basal area (m^2)	28	30.34	33.16
Number of families	50	47	45
Number of genera	142	161	112
Number of species	237	279	148
Percentage of trees that belong to the top five most abundant species (%)	19.9	21.1	31.5
Percentage of trees in Urticaceae or Cecropiaceae (%)	0.3	0.3	6.8
Fisher's alpha diversity index	142.32	186.86	66.03
Shannon-Wiener diversity index (using Ln)	4.95	5.08	4.18
Simpson's inverse diversity index	80.76	70.87	25.16

The three plots differed in composition of the tree families that showed the highest importance values (sum of relative density and relative dominance). However,

Arecaceae (the palm family) was in the top five families of the highest importance values in all three plots. Myristicaceae, Sapotaceae, and Moraceae (the fig family) were in the top five families of the highest importance values in two plots (Table 4.2). These families dominated the tree family composition by occupying 44.64%, 43.71%, and 50.43% of the total importance values in Yutsuntsa, Juyuintsa, and Sawastian, respectively.

Table 4.2. The top five tree families with the highest importance values in the three 1-ha plots.

	Relative density (%)	Relative dominance (%)	Importance Value
Yutsuntsa			
Myristicaceae	10.59	12.48	23.07
Lecythidaceae	9.77	10.4	20.17
Sapotaceae	8.31	9.61	17.92
Moraceae	7.33	7.45	14.78
Arecaceae	6.68	6.65	13.33
Juyuintsa			
Arecaceae	17.44	12.26	29.7
Mimosaceae	7.84	10.05	17.89
Myristicaceae	5.44	9.72	15.16
Sapotaceae	4.16	8.26	12.42
Lauraceae	6.56	5.66	12.22
Sawastian			
Meliaceae	10.97	19.27	30.24
Bombacoideae (within Malvaceae)	20.86	8.28	29.14
Mimosaceae	7.55	9.2	16.75
Moraceae	3.24	12.83	16.07
Arecaceae	4.68	3.97	8.65

Likewise, the three plots were different in composition of the tree genera that had the highest importance values. However, *Inga* (in the legume family) appeared to be in the top five genera of the highest importance values in all three plots (Table 4.3). *Oenocarpus* (in the palm family) and *Virola* were in the top five genera of the highest importance values in two plots (Table 4.3). These genera dominated the tree genus composition by occupying 29%, 28.46%, and 33.73% of the total importance values in Yutsuntsa, Juyuintsa, and Sawastian, respectively.

Table 4.3. The top five tree genera with the highest importance values in the three 1-ha plots.

	Relative density (%)	Relative dominance (%)	Importance Value
Yutsuntsa			
Eschweilera (Lecythidaceae)	8.45	7.71	16.16
Iryanthera (Myristicaceae)	4.89	9.03	13.92
Oenocarpus (Arecaceae)	4.56	5.25	9.81
Inga (Mimosaceae)	4.07	5.11	9.18
Virola (Myristicaceae)	5.54	3.38	8.92
Juyuintsa			
Oenocarpus (Arecaceae)	7.68	6.63	14.31
Virola (Myristicaceae)	4	7.94	11.94
Iriartea (Arecaceae)	7.2	4.63	11.83
Inga (Mimosaceae)	5.44	4.38	9.82
Ocotea (Lauraceae)	4.8	4.22	9.02
Sawastian			
Matisia (Bombacoideae within Malvaceae)	17.81	4.93	22.74
Guarea (Meliaceae)	4.32	9.48	13.8

(Table 4.3 continued)

Inga (Mimosaceae)	6.47	5.63	12.1
Trichilia (Meliaceae)	5.58	4.13	9.71
Ficus (Moraceae)	0.36	8.74	9.1

Oenocarpus bataua, an arborescent palm species, was among the top five tree species in terms of high importance values in two plots (Table 4.4). Another arborescent palm species, *Iriartea deltoidea*, had the second highest importance value in Juyuintsa. In addition, two species in Myristicaceae (*Iryanthera macrophylla* and *Virola flexuosa*), Mimosaceae (*Inga* sp. and *Parkia velutina*), and Meliaceae (*Guarea kunthiana* and *Guarea macrophylla)* were among the top five tree species with the highest importance values in Yutsuntsa, Juyuintsa, and Sawastian, respectively (Table 4.4). These species dominated the tree species composition by respectively occupying 22.14%, 19.67%, and 24.33% of the total importance values in Yutsuntsa, Juyuintsa, and Sawastian. Appendix A shows a list of top 30 species in terms of importance values in the three plots.

Table 4.4. The top five tree species with the highest importance values in the three 1-ha plots.

	Relative density (%)	Relative dominance (%)	Importance Value
Yutsuntsa			
Iryanthera macrophylla	3.91	8.71	12.62
Eschweilera coriacea	6.84	5.53	12.37
Oenocarpus bataua	4.56	5.25	9.81
Micropholis egensis	2.12	3.89	6.01
Virola flexuosa	2.44	1.02	3.46
Juyuintsa			
Oenocarpus bataua	7.68	6.63	14.31
Iriartea deltoidea	7.2	4.63	11.83
Inga sp.	3.04	2.71	5.75
Parkia velutina	0.32	4.13	4.45

(Table 4.4 continued)

Himatanthus bracteatus	1.28	1.72	3
Sawastian			
Matisia lasiocalyx	17.09	4.48	21.57
Urera sp.	5.76	2.22	7.98
Guarea kunthiana	0.9	6.65	7.55
	3.24	2.8	6.04
Ficus ypsilophlebia	0.18	5.33	5.51

The three plots included 581 species/morphospecies among 1,787 individuals, suggesting a potential unique species for every three individuals. Sørensen's dissimilarity distance matrix for species abundance and presence/absence both indicated very little overlap in species composition between paired plots. Eighty-five to ninety-three percent of the species composition based on abundance matrices and 84-90% of the species composition based on presence/absence matrices between paired plots were dissimilar (Table 4.5). At the genus level, 50-72% of the genus composition using abundance data and 39-49% of the genus composition based on presence/absence differed between paired plots (Table 4.5). Moreover, the within-plot variation in species composition also indicated high levels of species dissimilarity between paired 20 X 20 m grids in all three plots. In Yutsuntsa and Juyuintsa, over 90% of the paired grids showed Sørensen's index of dissimilarity for > 0.8. Fewer paired grids (73%) in Sawastian had Sørensen's index of dissimilarity for > 0.8 (Figure 4.1).

Table 4.5. Sørensen's dissimilarity between paired plots based on A) abundance matrices and B) presence/absence matrices.

A.

	Species level				Genus level		
	Yutsuntsa	Juyuintsa	Sawastian		Yutsuntsa	Juyuintsa	Sawastian
Yutsuntsa	-			Yutsuntsa	-		
Juyuintsa	0.85	-		Juyuintsa	0.50	-	
Sawastian	0.93	0.86	-	Sawastian	0.72	0.62	-

B.

	Species level				Genus level		
	Yutsuntsa	Juyuintsa	Sawastian		Yutsuntsa	Juyuintsa	Sawastian
Yutsuntsa	-			Yutsuntsa	-		
Juyuintsa	0.85	-		Juyuintsa	0.39	-	
Sawastian	0.90	0.84	-	Sawastian	0.49	0.42	-

Figure 4.1. Frequency distribution of Sørensen's index of dissimilarity between paired grids within each of the three plots.

Ordination within and among three 1-ha plots

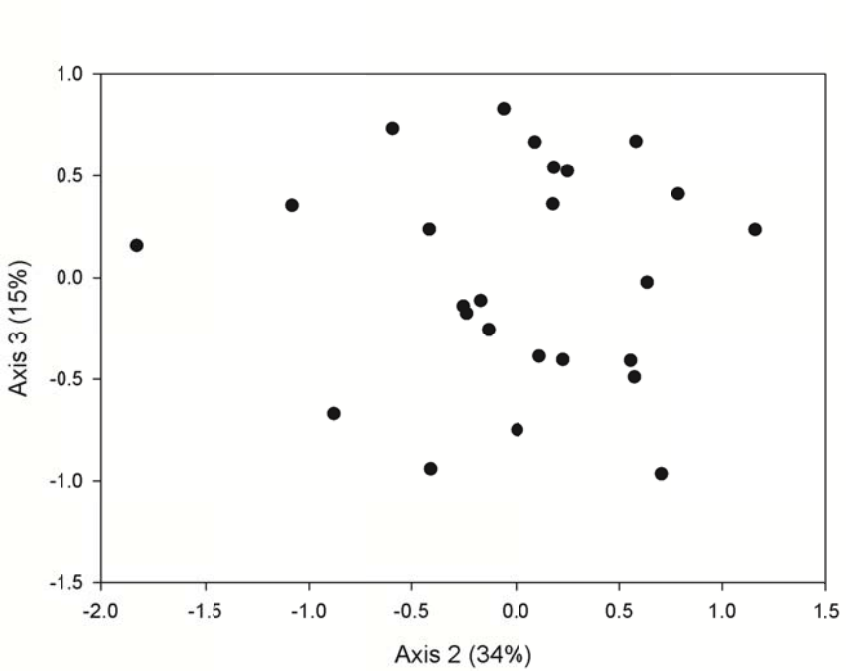
In this section I describe plot-based ordination patterns that were used to characterize potential species assemblages based on floristic composition. Species composition assemblages were found at between-plot level but not at within-plot level in the three plots. The Non-metric Multidimensional Scaling (NMS) ordination using Sørensen's similarity distance matrix based on species abundance suggested that within-plot grids did not show strong similarity with one another in ordination space in Yutsuntsa, Juyuintsa, or Sawastian. Overall, the three-dimensional axes explained 60% (stress = 19, instability = 0.0002, $p < 0.05$), 59% (stress = 18, instability = 0.0006, $p < 0.05$), and 82% (stress = 15.6, instability = 0.0005, $p < 0.05$) of the data variance for

Yutsuntsa, Juyuintsa, and Sawastian, respectively. Visual inspections of the ordination axes suggested that none of the within-plot grids in Yutsuntsa (Figure 4.2A), Juyuintsa (Figure 4.2B), or Sawastian (Figure 4.2C) showed distinctive clusters in ordination space. Likewise, at the genus level the three-dimensional NMS did not reveal within-plot clustering of the grids in Yutsuntsa (stress = 18.8, instability = 0.0003, $p < 0.05$), Juyuintsa (stress = 17.41, instability = 0.01, $p < 0.05$), or Sawastian (stress = 15.26, instability = 0.0009, $p < 0.05$). However, the NMS ordination of Sørensen's similarity distance matrix using species abundance in all 75 grids in the three plots detected clustering of the original data. The three-dimensional axes explained 73% of variance of the data (stress = 17.5, instability = 0.0001, $p < 0.05$). Visual inspection of the ordination axes demonstrated three distinctive groups of grids that were respectively located in the Yutsuntsa, Juyuintsa, and Sawastian plots (Figure 4.2D).

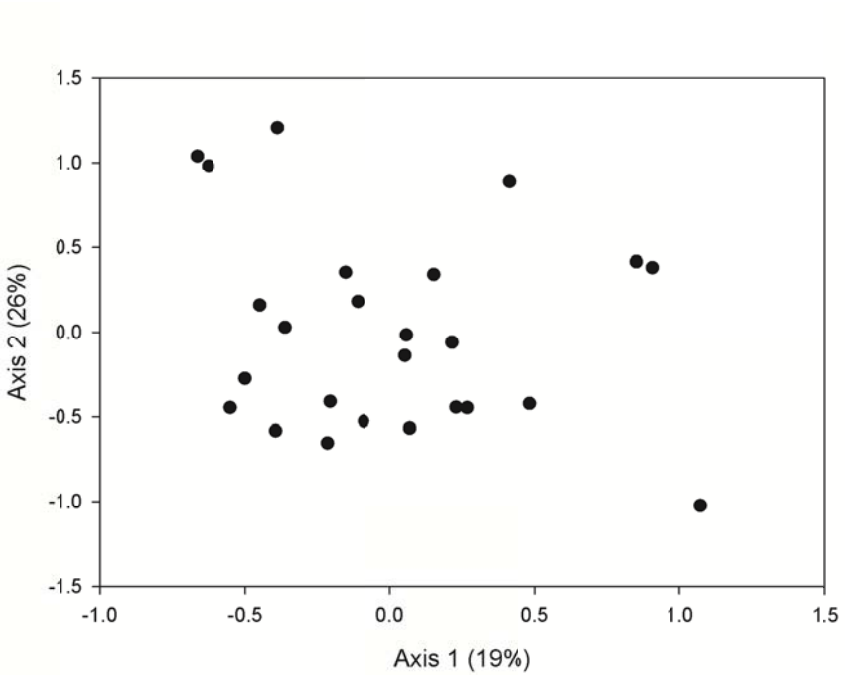
Neither visual inspections of the ordination graphs nor Kendall's Tau correlations with the ordination axes showed strong associations between ordination of the within-plot grids or all 75 grids from the three plots vs. the environmental variables. Specifically, at the species level the highest Kendall's Tau correlations among the three ordination axes ranged from -0.23 to -0.06 in Yutsuntsa, -0.34 to 0.37 in Juyuintsa, -0.23 to 0.27 in Sawastian, and -0.27 to 0.39 for all three plots (Table 4.6). Similarly, at the genus level few environmental variables had strong correlations with the NMS ordination axes. Kendall's Tau correlations ranged from -0.14 to 0.04 in Yutsuntsa, -0.28 to 0.4 in Juyuintsa, and -0.42 to 0.24 in Sawastian.

Figure 4.2. NMS ordination scores of the two axes explaining the highest percentage variances of the data in Yutsuntsa (A), Juyuintsa (B), Sawastian (C), and all three plots (D). Value in the parenthesis indicates the percentage variance explained by the axis.

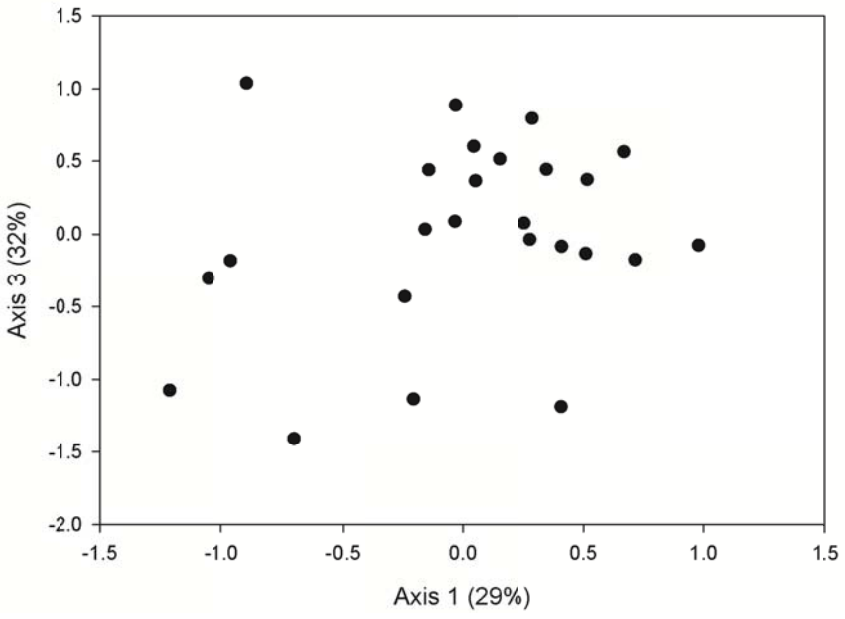
A.



B.


1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
Axis 2 (26%)
-1.0
-0.5
0.0
0.5
1.0
1.5
Axis 1 (19%)

C.


1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
Axis 3 (32%)
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
Axis 1 (29%)

D.

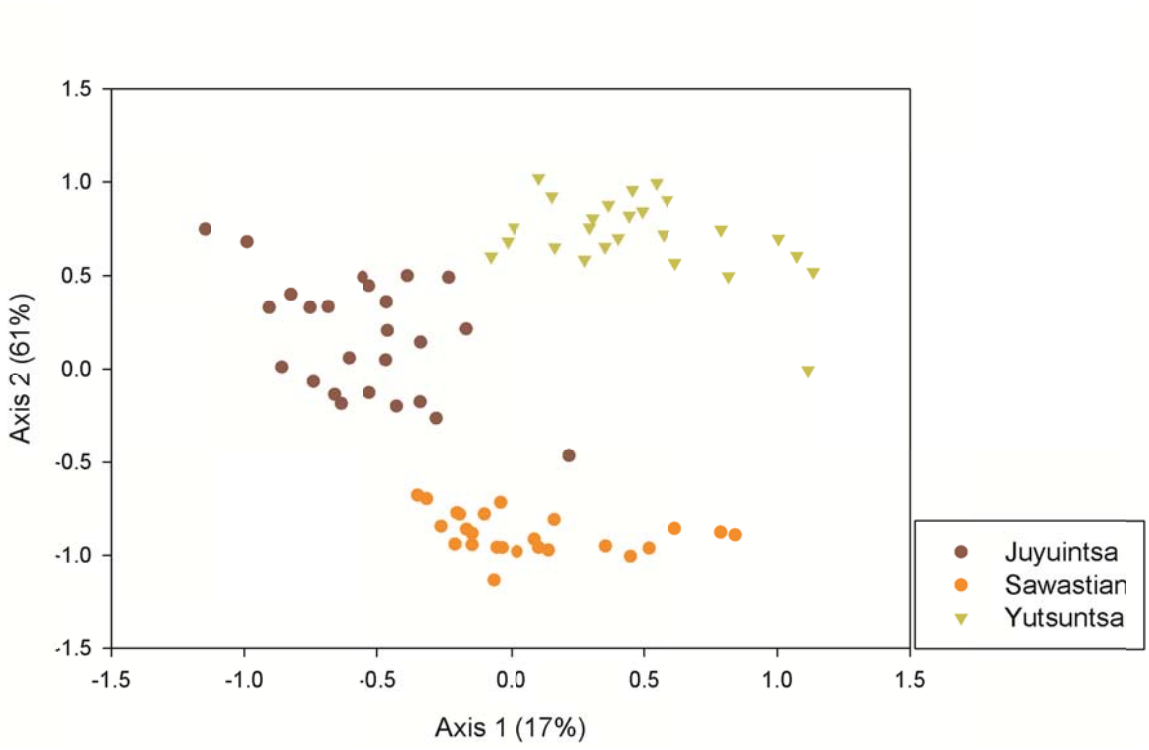


Table 4.6. Kendall's Tau correlations between the ordination axes and the environmental variables. Only the highest/lowest Tau value is shown for each variable.

Environmental variable	Yutsuntsa	Juyuintsa	Sawastian	All 3 plots
% canopy openness	-0.23	-0.16	-0.06	-0.27
Leaf area index 1	0.11	0.09	0.27	0.39
Soil moisture	N/A	-0.34	-0.1	N/A
Soil temperature	N/A	0.14	-0.23	N/A
Soil pH	N/A	0.35	0.12	N/A
Slope	N/A	-0.23	0.14	N/A
Soil color	N/A	0.37	0.12	N/A
Soil color chroma	N/A	0.13	-0.14	N/A

Mantel tests and indicator species analysis

In this section I aim to elucidate how species composition patterns were associated with the biophysical environment and if certain species were consistently found in habitats of particular environmental attributes. Despite the low correlations among environmental variables and ordination axes (see above), there appeared to be congruence between the Euclidian distance matrices of certain environmental variables and Sørensen's species dissimilarity distance matrices using both abundance and presence/absence data even though the correlations were surprisingly low. Species composition in Yutsuntsa was significantly correlated with percentage canopy openness and leaf area index (Table 4.7). In Juyuintsa only the data matrices using presence/absence showed significant correlations with soil moisture and pH (Table 4.7). Percentage canopy openness and soil color were significantly correlated to species composition using abundance data, whereas leaf area index, slope, and soil color were significantly correlated to species composition using presence/absence data (Table 4.7). The species similarity distance matrix combining abundance data of all three plots had significant correlations with leaf area index (Table 4.7). Nevertheless, the Mantel tests at the genus level using abundance data did not reveal any significant correlations between environmental variables and genus composition. Only percentage canopy openness in Sawastian, leaf area index in Yutsuntsa, soil pH in Juyuintsa, and soil color in Sawastian showed low correlations ($p < 0.1$) with the genus abundance matrices (Table 4.8).

Table 4.7. Mantel correlations (*r* values) between species composition using abundance and presence/absence data vs. environmental variables. * = p <0.1; ** = p < 0.05; *** = p < 0.01.

	Species abundance				Species presence		
	Yutsuntsa	Juyuintsa	Sawastian	All 3 plots	Yutsuntsa	Juyuintsa	Sawastian
Environmental variable							
% canopy openness	0.14*	-0.03	-0.2**	-0.01	0.15**	-0.03	-0.11
Leaf area index	0.28**	0.04	0.13	0.3***	0.26**	-0.003	0.05
Soil moisture	N/A	0.04	0.02	N/A	N/A	0.13**	0.09
Soil temperature	N/A	-0.002	0.08	N/A	N/A	0.06	-0.07
Soil pH	N/A	0.06	-0.07	N/A	N/A	0.2**	-0.01
Slope	N/A	-0.1	0.05	N/A	N/A	0.06	-0.18**
Soil color	N/A	0.03	-0.13**	N/A	N/A	-0.005	-0.1*
Soil color chroma	N/A	-0.006	-0.08	N/A	N/A	-0.06	-0.11

Table 4.8. Mantel correlations (*r* values) between genus composition using abundance data vs. environmental variables. * = p <0.1.

	Yutsuntsa	Juyuintsa	Sawastian
Environmental variable			
% canopy openness	0.04	-0.07	-0.2*
Leaf area index	0.17*	-0.06	0.13
Soil moisture	N/A	0.07	0.05
Soil temperature	N/A	-0.07	0.2
Soil pH	N/A	0.15*	-0.08
Slope	N/A	-0.001	0.06
Soil color	N/A	0.04	-0.12*
Soil color chroma	N/A	-0.12	-0.09

Gentry (1988) claimed that tropical tree communities are predictable in their floristic composition and diversities and that the predictability is often drawn from environmental parameters. I conducted indicator species analysis to examine whether or not environmental heterogeneity might show promise of separating species by their environmental niches. Indicator species analysis identified nine species in Yutsuntsa, 26 species in Juyuintsa, 23 species in Sawastian, and 16 species in all three plots with a slightly significant ($p < 0.1$) indicator value for higher or lower bounds of different environmental variables (Table 4.9). Two canopy palm species, *Oenocarpus bataua* and *Iriartea deltoidea*, were significantly associated with greater light availability (higher percentage canopy openness and lower leaf area index) in Yutsuntsa. In contrast, *Iriartea deltoidea* was significantly associated with higher leaf area index in Juyuintsa. *Micropholis guyanensis* in Juyuintsa also had significant associations with higher percentage canopy openness and lower leaf area index. *Trichilia pittieri* was found in association with lower percentage canopy openness and higher leaf area index in Sawastian and in all three plots combined (Table 4.9). Two species in

Juyuintsa were significantly associated with more than one soil characters: *Guarea kunthiana* with lower soil moisture and high soil pH and *Matisia lasiocalyx* with lower soil temperature and soil color with higher intensity (chroma). Likewise, there were two species in Sawastian with more than one association with soil characters: *Guarea macrophylla* with higher soil moisture and lower soil pH, and *Inga* sp.17 with lower soil pH and darker soil color (Table 4.9).

Table 4.9. Results of indicator species analysis (based on species abundance) for associations with environmental variables. * = $p < 0.1$, ** = $p < 0.05$, *** = $p < 0.01$. H or L represents higher (H) or lower (L) value of the environmental variable. Soil color at lower level indicated low lightness. Soil chroma at lower level indicated low intensity of soil color.

	Species	Indicator value	Environmental variable value
Yutsuntsa			
% canopy openness	*Oenocarpus bataua*	52.2*	H
	Endlicheria aff. *formosa*	25*	H
	Posoqueria sp.1	25*	H
Leaf area index	*Iriartea deltoidea*	53.4***	L
	Cordia hebeclada	39.1*	H
	Naucleopsis sp.	38.5**	H
	Miconia punctata	25*	L
	Tapirira guianensis	25*	L
	Miconia punctata	25*	L
Juyuintsa			
% canopy openness	*Micropholis guyanensis*	30.8*	H
	Ocotea longifolia	30.8*	H
	Virola pavonis	25*	L
Leaf area index	*Iriartea deltoidea*	62.9***	H
	Himatanthus bracteatus	40.2*	L
	Micropholis guyanensis	36.4**	L
	Guarea pterorhachis	36.3*	H
	Inga sp.15	27.3*	L
	Matisia sp.1	27.3*	L

(Table 4.9 continued)

Soil moisture	*Siparuna decipiens*	41.4**	L
	Guarea kunthiana	36.4**	L
	Ocotea sp.3	27.3*	L
	Caryodendron orinocense	27.3*	L
Soil temperature	*Guarea* sp.	36.4**	L
	Matisia lasiocalyx	35.8*	L
	Himatanthus bracteatus	34.6**	L
	Browneopsis ucayalina	27.3*	L
	Pseudolmedia laevigata	27.3*	L
Soil pH	*Siparuna decipiens*	33.9*	H
	Guarea kunthiana	30.8*	H
Slope	*Matisia lasiocalyx*	40.6*	L
	Ocotea sp.3	25*	L
	Zygia sp.2	25*	L
	Virola pavonis	25*	L
Soil color	*Guatteria* sp.2	35.7**	Level 3
	Virola pavonis	30*	Level 4
	Virola sp.3	30*	Level 4
Soil chroma	*Couepia* sp.	100***	Level 6
	Inga auristellae	71.8***	Level 6
	Matisia lasiocalyx	63.3**	Level 6
	Chrysochlamys bracteolata	50**	Level 2
	Parkia velutina	50**	Level 2
	Clarisia racemosa	43.7**	Level 2
	Theobroma subincanum	42.9**	Level 4
	Oenocarpus bataua	40.6*	Level 2
Sawastian			
% canopy openness	*Trichilia pittieri*	60.8***	L
	Chimarris glabriflora	38*	L
	Sloanea grandiflora	27.3*	L
Leaf area index	*Trichilia pittieri*	48.4**	H
	Guarea macrophylla	47.2*	L
	Trichilia pittieri	44.1**	H
	Inga sp.20	35.2*	L
	Dendropanax arboreus	33.3**	L
	Theobroma cacao	30.8*	H
	Dialium guianense	25*	L
Soil moisture	*Guarea macrophylla*	56.4**	H

(Table 4.9 continued)

	Guarea kunthiana	40**	L
Soil temperature	*Sterculia apetala*	97.2***	L
	Bixa platycarpa	50*	L
	Coccoloba aff. *coronata*	50*	L
	Diospyros sp.	50*	L
	Piper reticulatum	50*	L
	Pourouma petiolulata	50*	L
	Sapium glandulosum	50*	L
Soil pH	*Guarea macrophylla*	60**	L
	Inga sp.17	30**	L
	Sloanea grandiflora	30**	L
	Sorocea steinbachii	30**	L
Slope	*Trichilia pittieri*	48.4**	H
	Urera sp.	42.7*	L
Soil color	*Inga* sp.17	30**	Level 3
Soil chroma	*Terminalia oblonga*	67.5**	Level 1
	Acacia glomerosa	64.6**	Level 4
	Pseudolmedia sp.2	50*	Level 4
All 3 plots			
% canopy openness	*Trichilia pittieri*	18.1**	L
	Guarea kunthiana	14.6*	H
	Trichilia septentrionalis	13.5*	H
Leaf area index	*Himatanthus bracteatus*	15.2**	L
	Trichilia pittieri	15.6*	H
	Dendropanax arboreus	14.3**	L
	Acacia glomerosa	13.3**	L
	Naucleopsis sp.	12.5**	H
	Theobroma cacao	12.5**	H
	Inga sp.20	12.2*	L
	Guatteria sp.2	12.2*	L
	Micropholis guyanensis	11.4**	L
	Matisia sp.1	11.4**	L

Twelve genera in Yutsuntsa, 42 in Juyuintsa, and 24 in Sawastian showed significant ($p < 0.1$) indicator values for higher or lower bounds of different environmental variables (Table 4.10). Two palm genera in Yutsuntsa, *Oenocarpus* and

Iriartea, were indicative of higher percentage canopy openness and lower leaf area index. In contrast, *Iriartea* in Juyuintsa was a significant indicator genus of higher leaf area index. *Inga*, *Sterculia*, *Matisia*, and *Micropholis* in Juyuintsa were identified as indicator genera for higher percentage canopy openness and lower leaf area index (Table 4.10). The palm genera of *Wettinia* and *Oenocarpus* in Juyuintsa and *Iriartea* in Sawastian were significant indicators for lower soil pH, lower soil moisture, or medium soil color lightness and intensity. *Guatteria* and *Protium* in Juyuintsa, along with *Inga* in Sawastian, had significant associations with greater soil moisture and lower soil pH (Table 4.10).

Table 4.10. Results of indicator species analysis (based on genus abundance) for associations with environmental variables. * = $p < 0.1$, ** = $p < 0.05$, *** = $p < 0.01$. H or L represents higher (H) or lower (L) value of the environmental variable. Soil color at lower level indicated low lightness. Soil chroma at lower level indicated low intensity of soil color.

	Genus	Indicator value	Environmental variable value
Yutsuntsa			
% canopy openness	*Oenocarpus*	52.5*	H
	Protium	47.5*	L
	Mouriri	44.3**	L
	Posoqueria	25*	H
	Endlicheria	25*	H
Leaf area index	*Iriartea*	53.4***	L
	Licania	46.4*	H
	Naucleopsis	40.6**	H
	Cordia	39.1*	H
	Brownea	25*	L
	Tapirira	25*	L
	Perebea	25*	L
Juyuintsa			
% canopy openness	*Inga*	60.7**	H
	Matisia	58.3**	H
	Ocotea	54.5*	H

(Table 4.10 continued)

	Sterculia	46.2***	H
	Micropholis	46.2***	H
	Pseudolmedia	30.8*	H
Leaf area index	*Iriartea*	64.6***	H
	Matisia	59.9**	L
	Inga	59.2*	L
	Micropholis	54.5***	L
	Guarea	53.5*	H
	Himatanthus	49**	L
	Sterculia	40.2*	L
	Licania	35.7**	H
Soil moisture	*Guatteria*	61.7***	H
	Protium	52.2***	H
	Siparuna	38**	L
	Eugenia	35.4*	H
	Casearia	27.3*	L
	Caryodendron	27.3*	L
Soil temperature	*Matisia*	53*	L
	Pseudolmedia	36.4**	L
	Browneopsis	27.3*	L
Soil pH	*Guarea*	51.9*	H
	Guatteria	49.9*	L
	Protium	41.4*	L
	Siparuna	41.3**	H
	Wettinia	35.2*	L
	Tovomito	25*	L
Slope	*Zygia*	41.5**	L
	Neea	30.8*	H
Soil color	*Oenocarpus*	63*	Level 3
	Protium	45.5*	Level 3
Soil chroma	*Couepia*	100***	Level 6
	Couratari	50*	Level 6
	Rhodostemonodaphne	50*	Level 6
	Duguetia	50*	Level 6
	Hyeronima	50*	Level 6
	Clarisia	43.7**	Level 2
	Chrysochlamys	42.9**	Level 2
	Parkia	42.9**	Level 2
	Oenocarpus	41*	Level 2

(Table 4.10 continued)

Sawastian			
% canopy openness	*Chimarris*	38*	L
	Sloanea	27.3*	L
Leaf area index	*Theobroma*	33.9*	H
	Dendropanax	33.3**	L
	Dialium	25*	L
Soil moisture	*Inga*	57.8*	H
Soil temperature	*Sterculia*	85.2**	L
	Iriartea	76.7*	L
	Bixa	50*	L
	Diospyros	50*	L
	Piper	50*	L
Soil pH	*Inga*	72.6***	L
	Sloanea	30**	L
	Sorocea	30**	L
Slope	*Trichilia*	72.6***	H
	Urera	42.7*	L
	Ocotea	33.3**	L
	Cordia	25*	L
Soil color	*Sterculia*	45*	Level 3
Soil chroma	*Terminalia*	67.5**	Level 1
	Acacia	64.6**	Level 4
	Diospyros	50*	Level 4
	Piper	50*	Level 4
	Phytelephas	44.3*	Level 4

Multiple regressions

In this section I demonstrate how a collection of environmental attributes were associated with species composition patterns. Multiple regression analyses were used to evaluate the relative influences of multiple environmental factors on floristic composition at both species and genus levels. The analyses obtained strong models for Yutsuntsa at the species level using abundance data and moderate models for Yutsuntsa and Juyuintsa at the species level using presence/absence data. Ninety-two

percent of the variability in species abundance in Yutsuntsa could be accounted for by a combination of percent canopy openness and leaf area index in descending order of importance (Table 4.11). This model remained nearly unchanged when presence/absence data were used, and was only slightly weaker (64% of the variability was accounted for). In Juyuintsa, a combination of soil moisture and soil pH in the model accounted for 40% of the variability in species presence/absence (Table 4.11). Models in Sawastian at the species level and in all three plots at the genus level performed weakly (Table 4.11).

Table 4.11. Multiple regression models using only the environmental factors that showed significant correlations with the floristic composition in the Mantel tests. * = $p < 0.1$, ** = $p < 0.05$, *** = $p < 0.01$.

Level	Plot	Regression on matrices model	R^2
Species Abundance	Yutsuntsa	0.07 + 0.6 (% canopy openness***) + 0.03 (leaf area index***)	0.92***
	Juyuintsa	N/A	N/A
	Sawastian	0.83*** - 0.02 (% canopy openness***) - 0.05 (soil color**)	0.06***
	3 plots	0.840 + 0.03 (leaf are index 1**) + 0.12 (leaf area index***)	0.05***
Species presence/absence	Yutsuntsa	0.08 + 0.52 (% canopy openness***) + 0.13 (leaf area index***)	0.64***
	Juyuintsa	0.31 + 0.09 (soil moisture***) + 0.07 (soil pH***)	0.4***
	Sawastian	0.85*** - 0.04 (leaf area index*) - 0.04 (slope**) - 0.03 (soil color*)	0.06***
Genus Abundance	Yutsuntsa	0.64 + 0.01 (leaf area index***)	0.03***
	Juyuintsa	0.48 + 0.03(soil pH***)	0.16***
	Sawastian	0.76*** - 0.02 (% canopy openness***) - 0.05 (soil color**)	0.05***

Spatial point patterns of trees

In this section I describe plot-based point patterns of tree spatial distributions in terms of their clustering/dispersion along distances, as well as their spatial associations with one another. Overall, at the plot level, tree locations in Yutsuntsa, Juyuintsa, and Sawastian showed little significant spatial clustering or dispersion at a range of distances. The global transformed Ripley's K function (L_{Hat}) detected significant dispersion at the lag distances of 4-10 m in Yutsuntsa, also at 2-4 m and 20-26 m in Sawastian. No significant clustering or dispersion compared to complete spatial randomness occurred in Juyuintsa. Canopy trees in Yutsuntsa showed significant dispersion at short lag distances of 4-8 m whereas canopy trees in Juyuintsa and Sawastian were insignificantly clustered at all lag distances. In contrast to canopy trees, subcanopy trees in Yutsuntsa were significantly clustered at distances of 16-26 m. Although the subcanopy trees in Juyuintsa did not show significant dispersion, significant dispersion was detected at distances of 2-4 m and 20-26 m in Sawastian. Dispersion indices using tree abundance in each within-plot grid indicated little clumped distribution. Index of dispersion, Green's index, and Morisita's index for grids in all three plots were barely higher than their expected values when points are under a random distribution (Table 4.12).

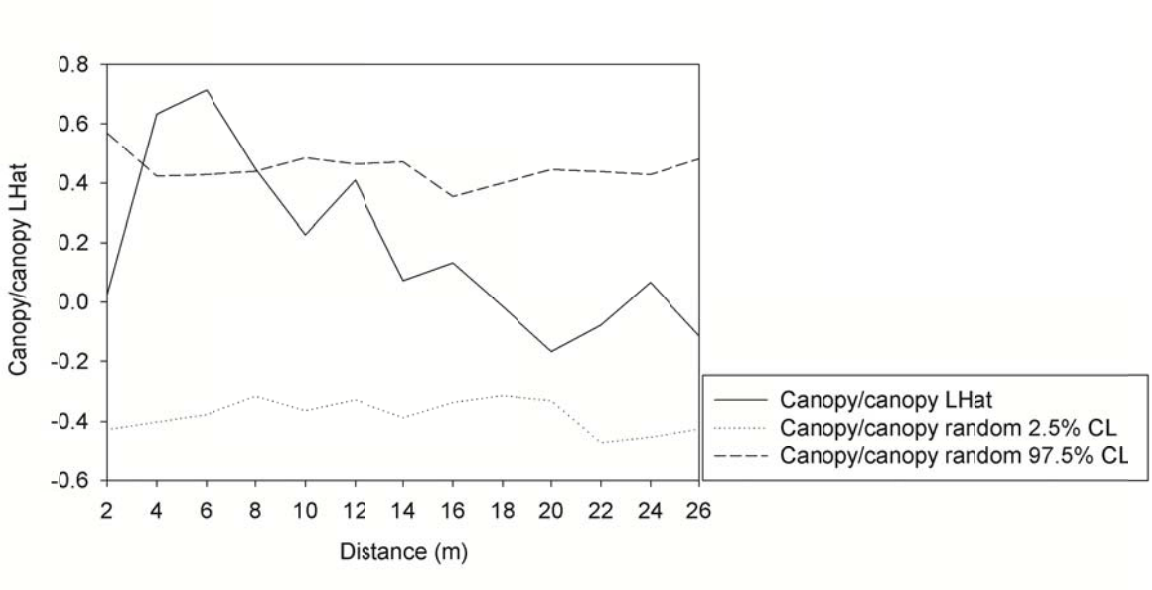
Table 4.12. Dispersion indices at the grid level.

Plot	Index of dispersion	Green's index	Morisita's index
Yutsuntsa	1.1 ($p > 0.05$)	0.004	1.004
Juyuintsa	1.22 ($p > 0.05$)	0.009	1.009
Sawastian	1.36 ($p > 0.05$)	0.02	1.02

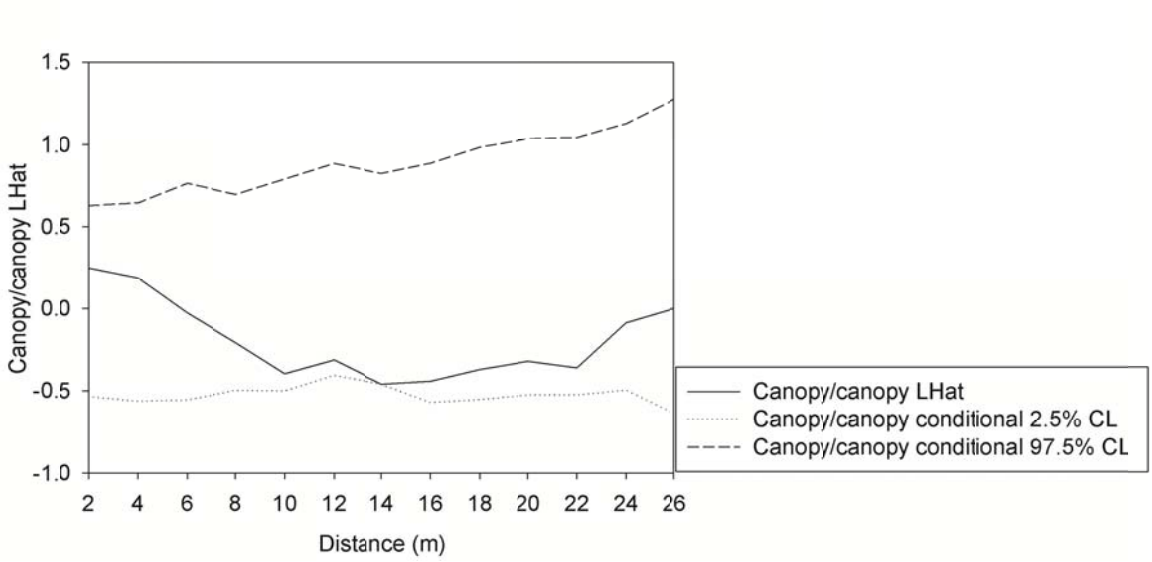
The bivariate second-order analysis, which tested the spatial associations between canopy vs. canopy, subcanopy vs. subcanopy, and subcanopy vs. canopy trees at lag distances, revealed different patterns among the three bivariate contrasts. There was significant dispersion (repulsion) between canopy trees in Yutsuntsa only at the lag distances of 4-6 m (Figure 4.3A). Non-significant clustering (attraction) existed between canopy trees in Juyuintsa and Sawastian (Figure 4.3B, C). Spatial attractions were more prominent between subcanopy trees. Local transformed Ripley's K detected significant attractions at distances of 12-26 m in Yutsuntsa and at 22-26 m in Juyuintsa and non-significant attraction in Sawastian (Figure 4.4A, B, C). The associations between subcanopy vs. canopy trees differed among the three plots. Significant repulsion occurred at 14-26 m in Yutsuntsa whereas significant attraction was found at 10-26 m in Juyuintsa (Figure 4.5A, B). Subcanopy and canopy trees showed non-significant attraction in Sawastian (Figure 4.5C).

Figure 4.3. Bivariate transformed Ripley's K (L_{Hat}) and confidence envelopes for canopy vs. canopy trees in A) Yutsuntsa, B) Juyuintsa, and C) Sawastian. CL = confidence limit.

A.



B.


1.5
1.0
0.5
0.0
-0.5
-1.0
Canopy/canopy LHat
2 4 6 8 10 12 14 16 18 20 22 24 26
Distance (m)
Canopy/canopy LHat
Canopy/canopy conditional 2.5% CL
Canopy/canopy conditional 97.5% CL

C.

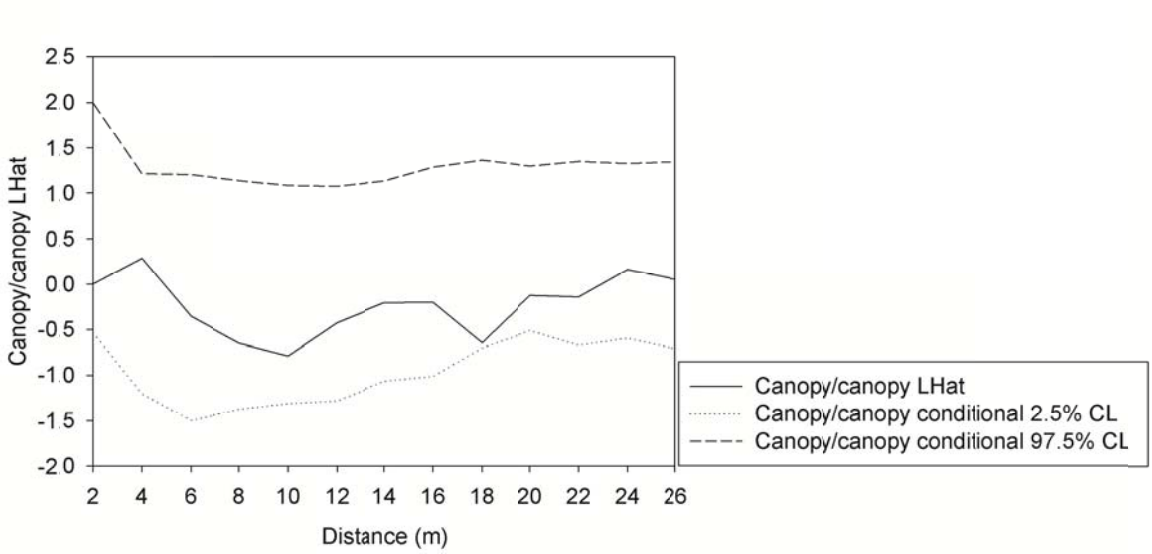
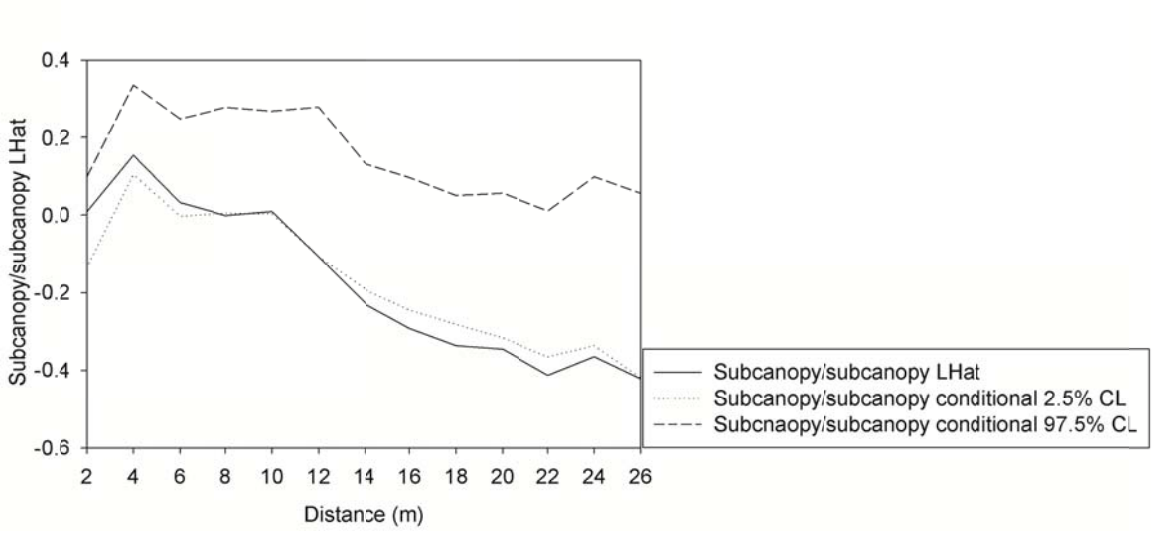
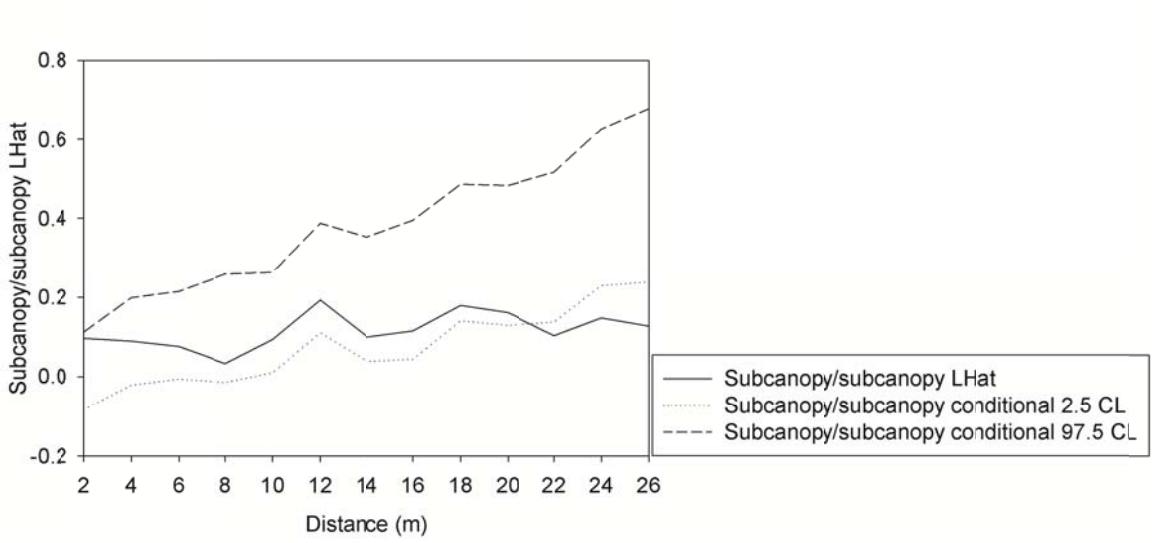

2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
Canopy/canopy LHat
2 4 6 8 10 12 14 16 18 20 22 24 26
Distance (m)
Canopy/canopy LHat
Canopy/canopy conditional 2.5% CL
Canopy/canopy conditional 97.5% CL

Figure 4.4. Bivariate transformed Ripley's K (L_{Hat}) and confidence envelopes for subcanopy vs. subcanopy trees in A) Yutsuntsa, B) Juyuintsa, and C) Sawastian. CL = confidence limit.

A.



B.



C.

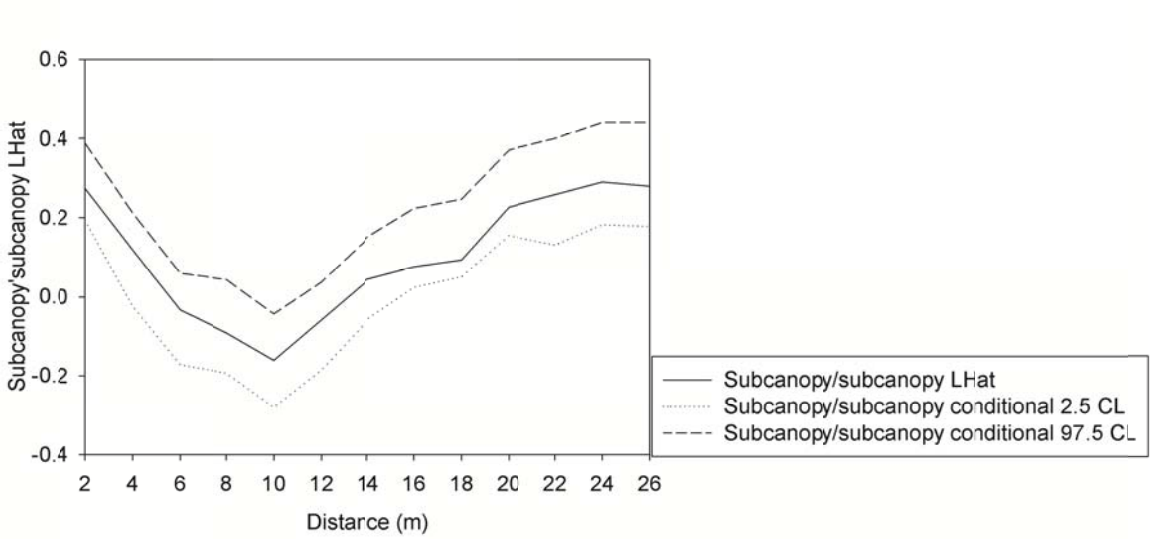
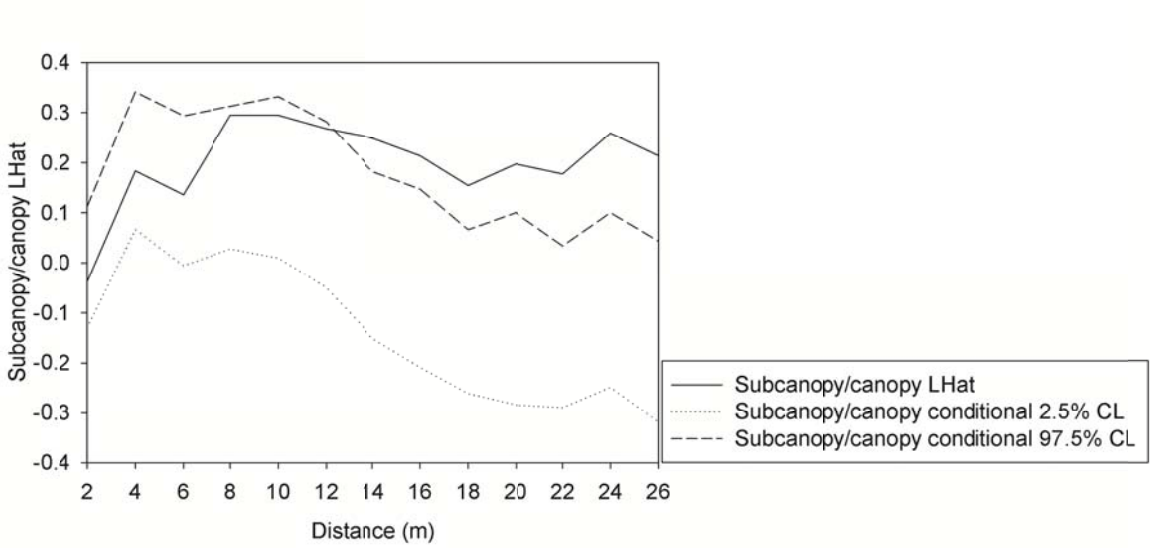
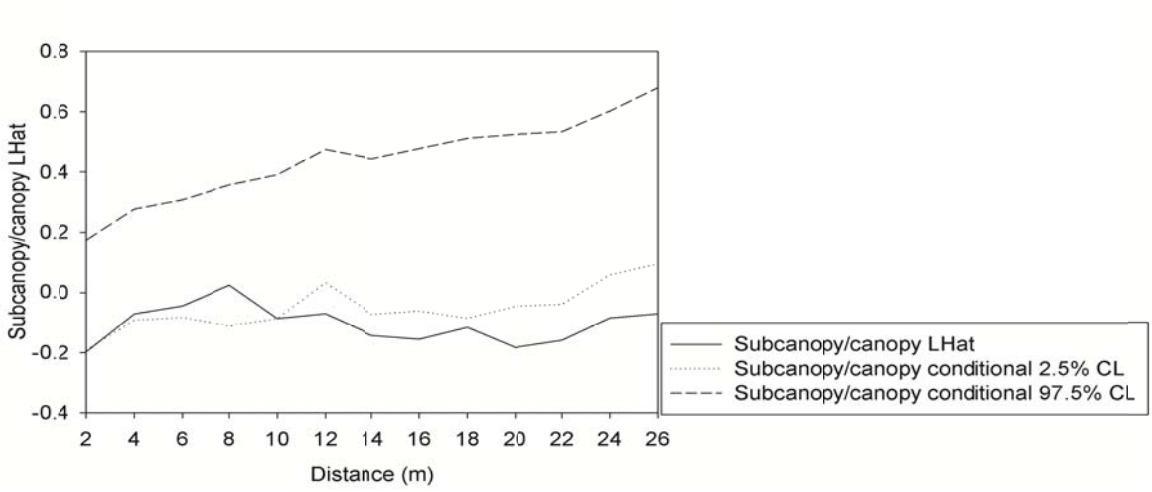


Figure 4.5. Bivariate transformed Ripley's K (L_{Hat}) and confidence envelopes for subcanopy vs. canopy trees in A) Yutsuntsa, B) Juyuintsa, and C) Sawastian. CL = confidence limit.

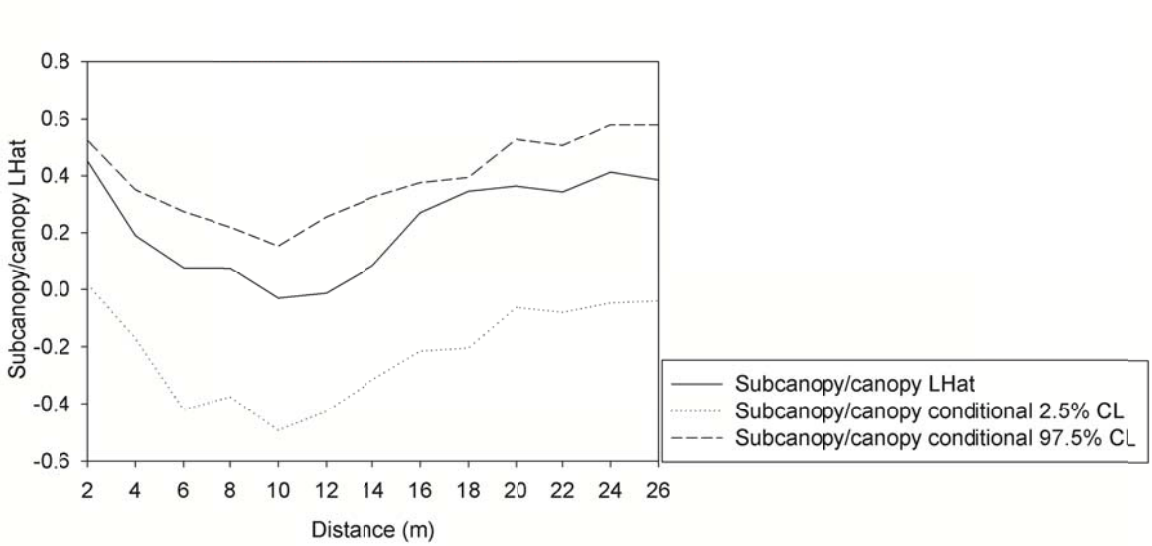
A.



B.



C.



Spatial autocorrelation of trees

In addition to examining spatial point patterns of individual trees, spatial autocorrelation analyses were conducted in order to detect spatial clustering or dispersion of tree characteristics (DBH and height), which are also constituents of biodiversity

features. The estimation of global spatial autocorrelation using Moran's I suggested that the spatial clusters of tree DBH in Yutsuntsa occurred across the plot at the distance lags of 0-28 m, 42-56 m, 70-84 m, and 98-100 m (Z score > 1.96, $p < 0.05$). Geary's C only detected spatial clusters between 0-14 m (Z score > 1.96, $p < 0.05$). The overall correlograms for Moran's I and Geary's C were not significant (Bonferroni corrected $p > 0.05$). In Juyuintsa, no spatial clusters were detected (Z score < 1.96, $p > 0.05$). The overall correlograms for Moran's I and Geary's C were significant (Bonferroni corrected $p < 0.01$). The only spatial cluster in Sawastian was found between 70-84 m using Moran's I (Z score > 1.96, $p < 0.05$). The overall correlograms for Moran's I and Geary's C were not significant (Bonferroni corrected $p > 0.05$). Moran's I suggested that the spatial clusters of tree height in Yutsuntsa occurred across the plot at the distance lags of 0-28 m and 42-56 m (Z score > 1.96, $p < 0.05$). Geary's C only detected spatial clusters between 0-14 m and 42-56 m (Z score > 1.96, $p < 0.05$). The overall correlograms for Moran's I and Geary's C were highly significant (Bonferroni corrected $p < 0.001$). In Juyuintsa, tree height clusters were detected at lags of 0-42 m and 70-100 m according to Moran's I and at 0-14 m for Geary's C (Z score > 1.96, $p < 0.05$). The overall correlogram for Moran's I was highly significant (Bonferroni corrected $p < 0.001$). However, no spatial clustering in tree height was found in Sawastian.

DISCUSSIONS

The three 1-ha tree plots shared certain local alpha diversity patterns in common. The species-rich tree communities in southeastern Ecuador harbored some locally abundant species. Five of the most abundant tree species in Yutsuntsa, Juyuintsa, and Sawastian accounted for at least 20% of total tree abundance. In Sawastian, the high proportion of abundant trees (31.5%) was largely contributed by two most abundant

species: *Matisia lasiocalyx* (Bombacoideae) and a species in *Urera* (Urticaceae). Individuals of *Matisia lasiocalyx* accounted for 17% of total abundance whereas *Urera* accounted for 5.75%. *Matisia lasiocalyx* has been found in multiple regions of the lowland Amazon, including Amapá and Pará in Brazil, Napo and Pastaza in Ecuador, Loreto in Peru, and French Guiana. Specimen records also indicated that this species occurs in coastal Ecuador and Andean Colombia (Tropicos Database by the Missouri botanical Garden, http://www.tropicos.org/Name/3900439?tab=specimens). As a hummingbird-adapted species for pollination (Cotton 1998), *Matisia lasiocalyx* occurred in Sawastian in various sizes. The large percentage of *Matisia lasiocalyx* in Sawastian appeared to directly contribute to the less diverse tree communities compared to Yutsuntsa and Juyuintsa, but the mechanisms that influenced species abundance in Sawastian remains unknown. It is possible that because trees in Bombacoideae and Urticaceae are often associated with recent disturbances (K. R. Young and N. Pitman, personal communications), the plot in Sawastian might have experienced relatively more recent natural disturbance events (e.g. large tree fall gaps or wind blow down) than plots in Yutsuntsa or Juyuintsa. Furthermore, the plot is closer to Sawastian's community center (Table 3.1). Field observations and conversations with residents in Sawastian indicated that the plot did not experience recent anthropogenic disturbances (e.g. logging or farming), although occasional hunting activities may occur.

Yutsuntsa, Juyuintsa, and Sawastian harbored high species diversity compared to many other tropical rainforests. Specifically, all three forests had a Fisher's alpha diversity index greater than forests measured in Añangu (Ecuadorian), Las Tuxtlas (Mexico), La Selva (Costa Rica), and Barro Colorado Island (Panama). The last three forests are relatively well studied tropical sites (Table 4.13). Yutsuntsa and Juyuintsa in particular, were among the forests with the highest Fisher's alpha and Shannon-Wiener

diversity indices known at a 1-ha plot level in the world (Table 4.13). Even comparing the 1-ha plots of Yutsuntsa and Juyuintsa to other larger forests plots, the two forests still had diversity indices that were only slightly lower than in the 25-ha or 50-ha plots of Yasuní (Ecuador), Lambir (Malaysia), and Pasoh (Malaysia) (Table 4.13).

The great species richness in Yutsuntsa, Juyuintsa, and Sawastian are partially contributed by a large number of rare species and genera in those plots. At the species level, 56%, 59%, and 51% of the species in Yutsuntsa, Juyuintsa, and Sawastian, respectively, had only one individual in the entire 1-ha plot. Likewise, 27%, 34%, and 25% of the genera in Yutsuntsa, Juyuintsa, and Sawastian, respectively, had only one individual in the entire plot. On the other hand, the top five species with the highest importance values accounted for less than 50% of the total importance value in all three plots (Table 4.14). Compared to a few other tropical rainforests that harbored greater species diversity in larger inventory plots (e.g. plots in Lambir and Pasoh), to some extent lower percentages of species that have higher relative abundance and dominance may account for greater species diversity (Table 4.14).

Table 4.13. Comparisons among forest inventory plots in abundance, species richness, and diversity.

Site	Plot size (ha)	Number of trees	Number of species	Fisher's α	Shannon-Wiener (using log10)	Reference
Yutsuntsa	1	610	237	142.43	2.15	
Juyuintsa	1	622	279	186.86	2.21	
Sawastian	1	555	148	66.03	1.82	
Yasuní, Ecuador	25	17546	820	178	2.37	Valencia et al. 2004a
	1	702	251	141.7	2.11	Valencia et al. 2004a
(Ridge)	1	725	255	140		Valencia et al. 2004b
(Bottomland)	1	604	234	140.2		Valencia et al. 2004b
Cuyabeno, Ecuador	1	693	307	211		Leigh 1999
Añangu, Ecuador	1	734	153	58.8		Leigh 1999
Jatun Sacha, Ecuador	1	724	246	131.2		Leigh 1999
Cocha Cashu, Peru	1	650	189	89.5		Leigh 1999
Yanamono, Peru	1	580	283	218.2		Leigh 1999
Mishana, Peru	1	842	275	142.1		Leigh 1999
Bajo Calima, Columbia	1	664	252	148		Leigh 1999
Las Tuxtlas, Mexico	1	359	88	37.2		Leigh 1999
La Selva, Costa Rica	4.4	1838	172	46.4		Leigh 1999
Barro Colorado Island, Panama	50	21205	227	35.4	1.86	Leigh et al. 2004
	25	10728	206	36.1		Condit et al. 2004

(Table 4.13 continued)

	1	429	91	35.6	1.66	Leigh et al. 2004
Lambir, Malaysia	52	33175	1003	195.1	2.59	Lee et al. 2004
	25	15,916	851	193		Condit et al. 2004
	1	637	247	153.6	2.19	Lee et al. 2004
Pasoh, Malaysia	50	28,279	673	126.7	2.45	Manokaran et al. 2004
	25	13276	604	130		Condit et al. 2004
	1	531	206	125	2.15	Manokaran et al. 2004

Table 4.14. Relative abundance, basal area, and importance values of the top five species in forest inventory plots (other plot data obtained from Ashton et al. 2004).

Site	Relative density (%)	Relative dominance (%)	Importance Value
Yutsuntsa	19.87	24.4	44.27
Juyuintsa	19.52	19.82	39.34
Sawastian	27.17	21.48	48.65
Yasuní, Ecuador (25 ha)	16.9	10.1	27
Barro Colorado Island, Panama (50 ha)	24.4	41.9	66.3
Lambir, Malaysia (52 ha)	20	9.2	29.2
Pasoh, Malaysia (50 ha)	15	11.5	26.5

The distinctiveness of dry season may be one of the influential factors of species diversity in these tropical rainforests (Gentry 1988). The average precipitation of the driest quarter accounted for 17.8%-22% of the mean annual rainfall in Yutsuntsa, Juyuintsa, Sawastian, Yasuní, Lambir, and Pasoh. In contrast, only 5% of the annual rainfall accumulated during the driest quarter on Barro Colorado Island (Table 4.15). The lowest Fisher's alpha diversity index on Barro Colorado Island suggested that to some extent much reduced precipitation during dry season may result in stress in tropical forests and cause lowered species diversity. The absolute values of annual rainfall or rainfall for the driest quarter in Table 4.15 did not directly correspond to Fisher's alpha diversity index, indicating that the consistency and stability in precipitation all year around are more important than the amount of precipitation in maintaining species diversity. This finding supports Gentry (1988) that species richness in lowland Neotropical forests is tightly correlated with precipitation patterns.

Table 4.15. Rainfall and diversity index in forest inventory plots (study area's rainfall information obtained from the WorldClim database; other plot data obtained from Ashton et al. 2004).

Site	Annual rainfall (mm)	Average rainfall for the driest quarter (mm)	Fisher's α
Yutsuntsa	3009.00	622.00	142.43
Juyuintsa	2988.00	605.00	186.86
Sawastian	2718.00	597.00	66.03
Yasuní, Ecuador	3081.00	563.00	142
Barro Colorado Island, Panama	2551.00	131.00	36
Lambir, Malaysia	2664.00	498.00	154
Pasoh, Malaysia	1788.00	318.00	125

By comparing alpha diversity in the form of floristic composition at within- and between-plot levels, the extent to which species diversity varied at the scale of within 100 m vs. 100 km was revealed. The variation in floristic composition at the within-plot level was prominent in Yutsuntsa, Juyuintsa, and Sawastian (Figure 4.1). Sørensen's species dissimilarity revealed great difference in species composition between paired 20 X 20 m grids at a fine scale of within each plot in Yutsuntsa (0.61-1, mean = 0.86), Juyuintsa (0.65-1, mean = 0.85), and Sawastian (0.5-1, mean = 0.79). At the between-plot level, Yutsuntsa, Juyuintsa, and Sawastian shared little similarity in species composition between them. Sørensen's species dissimilarity index showed 85%-93% of variation in species composition, despite the fact that the geographic distance between plots only ranges from 35.4 to 119.8 km (Table 4.16). Although Sawastian may harbor a unique tree community caused by recent disturbances (see above), the undisturbed forests in Yutsuntsa and Juyuintsa still show 85% of difference in species composition and 50% in genus composition (Table 4.16). Other plots in northern Ecuador and the Peruvian Amazon showed higher species similarity between closer plots. Such pattern was also observed at the genus level with a lower degree of dissimilarity than at the species level (Table 4.16). Other tropical rainforest plots outside the Amazon shared low species similarity with other plots in the same region. Two tree plots that were only 1.5 km apart from each other in a rainforest in Costa Rica only shared 22% of species coincidence (Di Stefano et al. 1995). Three plots in a flooded Brazilian rainforest showed 45%-70% of species dissimilarity (Ferreira 1997). In some forests species similarity varied widely with clear distinction in dominant species among plots that differed in topography or lithology (e.g. Clark et al. 1999, Okuda et al. 2004).

Table 4.16. Sørensen's species or genus dissimilarity index between paired plots in the Amazon. Plot data in northeastern Ecuador and Loreto, Peru were provided by N. Pitman and O. Phillips.

Sites	Minimum	Maximum	Average
Species level			
3 plots in southeastern Ecuador	0.85	0.93	0.88
34 plots in northeastern Ecuador	0.44	0.99	0.8
12 plots in Loreto, Peru	0.52	0.99	0.85
Genus level			
3 plots in southeastern Ecuador	0.51	0.72	0.62
34 plots in northeastern Ecuador	0.32	0.94	0.64
12 plots in Loreto, Peru	0.32	0.91	0.67

Such substantial within- and between-plot heterogeneity in floristic variation might result from a few mechanisms that have been used for explaining potential species spatial aggregation. A combination of microhabitat and geographic distance may both contribute to the great heterogeneity in species composition. As a niche-based process, habitat association can result in spatial aggregation along an environmental gradient (Comita et al. 2007, Wiegand et al. 2007a). As a neutral process, dispersal limitation can give rise to spatial aggregation regardless of underlying habitat conditions or species (Hubbell et al. 1999, Plotkin et al. 2002). Reconciling the niche vs. neutral debate regarding the generating mechanism of species aggregation may provide signatures of what contributes to species coexistence and diversity (Lin et al. 2011, Condit et al. 2000). In this dissertation niche partitioning caused by potential interspecific competition could

not be examined due to the lack of temporal data. Therefore, the contribution of biological niche partitioning is not excluded as an explanatory feature.

The alpha diversity study in this dissertation included an exploratory analysis of species assemblages in ordination space. No obvious species assemblages were found within the plots in Yutsuntsa, Juyuintsa, and Sawastian according to the NMS ordination results. Furthermore, the low correlations between ordination axes and environmental variables suggested that local species assemblages (if there are any) may not be governed by the biophysical environment. The lack of species assemblages in ordination space and the weak correlations with biophysical environment implied that neutral processes, such as stochastic events or dispersal limitation, may be part of the generating mechanism of the floristic variation in species composition. Further examination is required to test the hypothesis of neutrality. In other Neotropical forests, Valencia et al. (2004) found that by using a two-ha subset of a 25-ha tree inventory data in Yasuní National Park in Ecuador, some habitat distinction in species richness exists but species richness could not be attributed to habitat segregation. Palmer et al. (2000) also found no relationships between the non-random clumping distribution of species richness and edaphic-topographic factors in a Costa Rican forest.

In contrast, strong species assemblages at the plot level corresponded to the relative geographic locations of Yutsuntsa, Juyuintsa, and Sawastian (Figure 4.2D). Three distinctive clusters that represented the three plots were located in ordination space in correspondence to the plot that is south of the Pastaza River (Sawastian) and the two plots north of Pastaza. The species assemblage in Juyuintsa was closer to Sawastian than Yutsuntsa, even though geographically Juyuintsa was farther from Sawastian than Yutsuntsa was. Floristically speaking, species that occurred in Yutsuntsa appeared to be rarer in the regional flora (M. Tirado, personal communication). Thus, the more unique

species composition in Yutsuntsa caused its species assemblage to be more distinguishable from the other two plots in ordination space. Other studies have shown that species assemblages in ordination space are related to topography, fragment size, bioclimatic types, drainage, and soil content (Thessler et al. 2005, Michalski et al. 2007, La Torre-Cuadros et al. 2007, Ramesh et al. 2010).

Not only were there no obvious within-plot species assemblages, but also there were only weak relationships between species and genus composition vs. light, topography, and soil characteristics in Yutsuntsa, Juyuintsa, and Sawastian. The weak or the lack of significant relationships between species/genus distance matrices and the Mantel test's *r* suggested that the biophysical environment, or at least the variables measured, may not impose species diversity patterns. Nevertheless, the influence of habitat association on species composition has been discovered in other Amazonian and tropical rainforests. In the Peruvian and Ecuadorian Amazon, tree composition has strong associations with topography, variation in soil type, and soil fertility (Svenning 1999, Tuomisto et al. 2003, Salovaara et al. 2005, Poulsen et al. 2006). Vegetation in other Latin American and Asian forests has shown relationships between alpha diversity and precipitation, temperature, vegetation index, soil, and topography (Potts et al. 2002, Okuda et al. 2004, Marcia et al. 2007, Ruokolainen et al. 2007, Jones et al. 2008). Perhaps the biophysical factors that influence species composition patterns were not measured in this study, which could potentially be soil chemical contents, soil fertility, or slope aspect. However, based on the aforementioned lack of species assemblages and the weak correlations with environmental variables, I propose that alpha diversity in the three 1-ha plots may partially arise at random and may be associated with stochastic events, as each species follows a random walk (Hubbell 2001, McGill 2003).

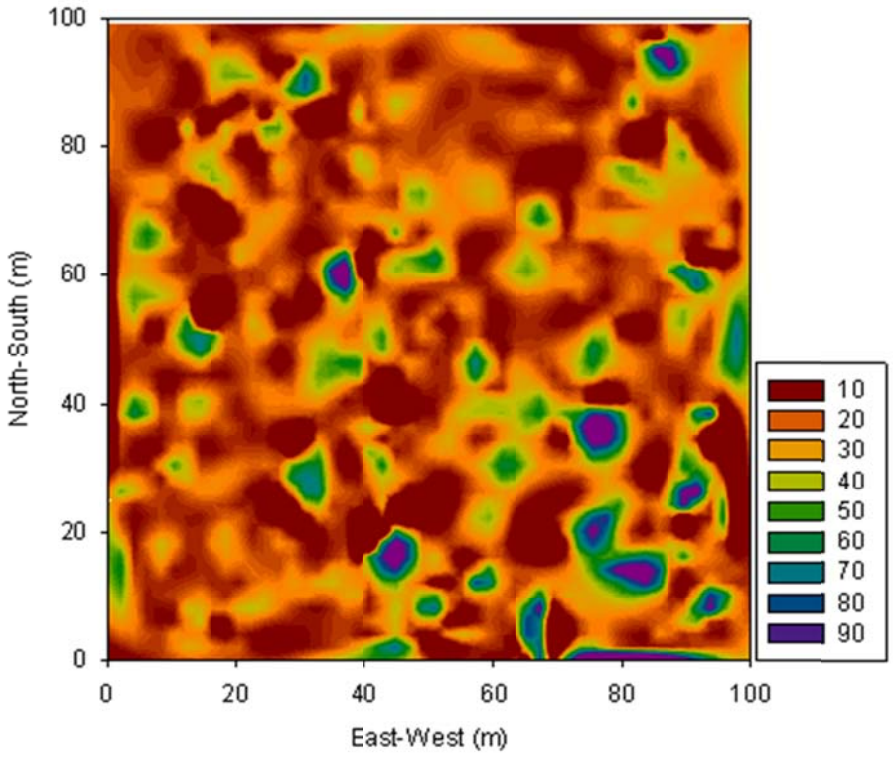
Perhaps variation in species composition in southeastern Ecuador could be better explained by geographic distance or other regional factors at a coarser scale. Mantel's *r* has shown significant relationships between geographic distance and species composition in some other tropical forests. Spatial variation explained more of the species composition in a Panamanian forest than environmental variables (Chust et al. 2006, Wiegand et al. 2007b). Floristic composition corresponded well to coarse-level forest types in the Brazilian Amazon (Wittmann et al. 2006, Emilio et al. 2010). Species composition for large-sized trees is more strongly related to geographic distance than edaphic variables in a tropical forest in Borneo (Potts et al. 2002).

By examining point-based distribution patterns of individual trees in within each plot, potential interactions with ecological processes and with other functional groups/species were indicated. Spatial point patterns in Yutsuntsa, Juyuintsa, and Sawastian showed a certain degree of correspondence with the distribution of tree size (DBH) and tree height. For all trees combined, the dispersion in Yutsuntsa and Sawastian occurred at where small and short trees were, except for a few tall trees in Sawastian. Dispersion of canopy trees in Yutsuntsa was observed at where small and short trees were found (Figure 4.6 and 4.7A, C). Spatial clustering of canopy trees in Yutsuntsa occurred in areas where trees in medium size and height were present, whereas the dispersion of canopy tree in Sawastian were in areas where mostly small and short trees occurred (Figure 4.6 and 4.7A, C). Dispersion (repulsion) between canopy trees in Yutsuntsa was found in areas where small and short trees were present. For the relationship between subcanopy trees, the clustering (attraction) was found in areas with trees in medium size and height in Yutsuntsa and Juyuintsa (Figure 4.6 and 4.7A, B). Repulsion between canopy and subcanopy trees in Yutsuntsa corresponded to the occurrence of trees in medium size and height, whereas attraction corresponded to locations of mostly small-

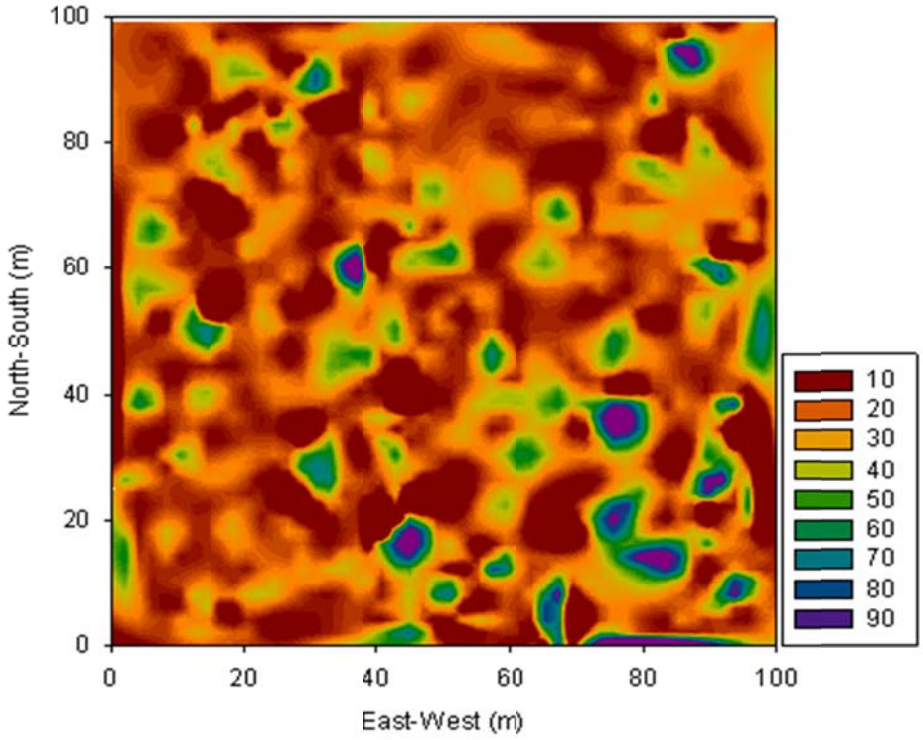
medium trees in Juyuintsa, with the exception of a few tall and large trees (Figure 4.6 and 4.7A, B). Franklin and Santos (2011) attributed repulsion between size classes to density-dependent mortality and attraction between smaller trees to patchy recruitment. A future closer examination on the spatial relationships between understory and subcanopy/canopy trees may shed light on tree point patterns that may be influenced by mortality and recruitment.

Figure 4.6. Interpolated distribution of tree DBH (cm) in the plots of Yutsuntsa (A), Juyuintsa (B), and Sawastian (C).

A.



B.


100
80
60
40
20
0
North-South (m)
0
20
40
60
80
100
East-West (m)
10
20
30
40
50
60
70
80
90

C.

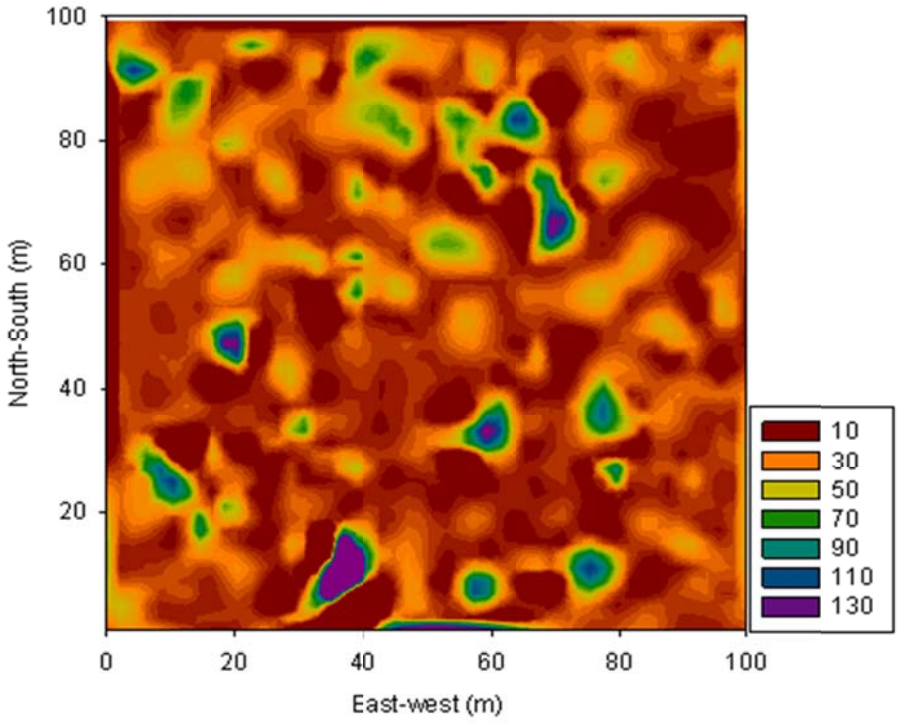
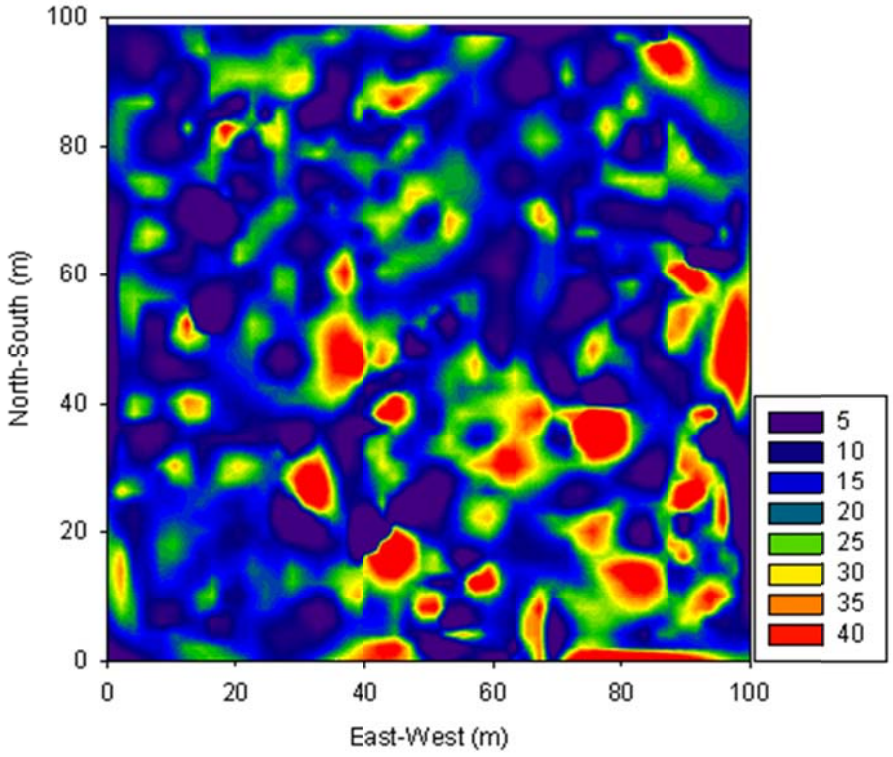
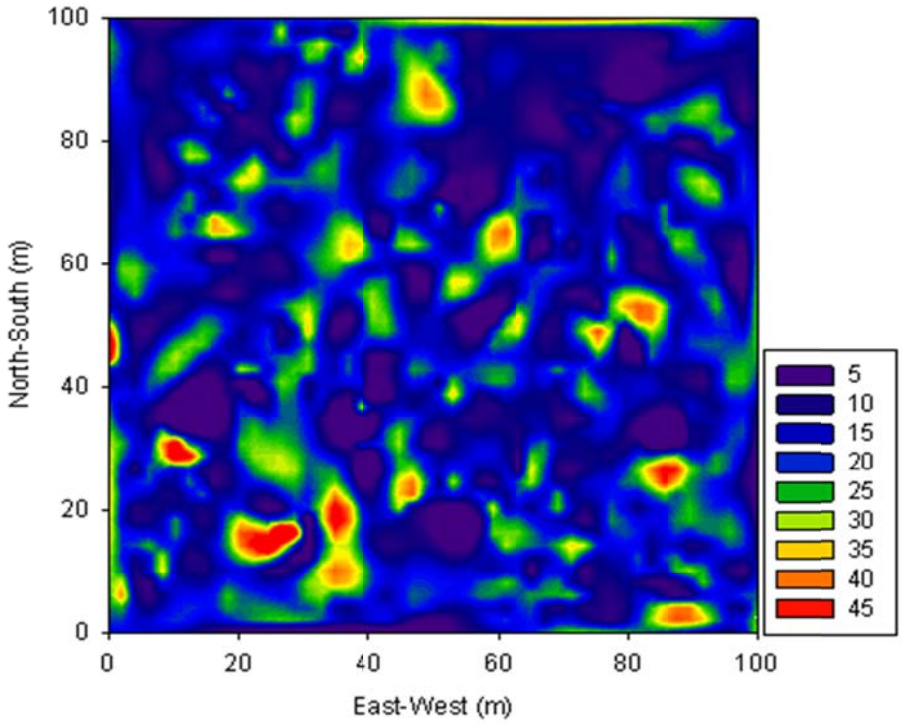

100
80
60
40
20
North-South (m)
0
20
40
60
80
100
East-west (m)
10
30
50
70
90
110
130

Figure 4.7. Interpolated distribution of tree height (m) in the plots of Yutsuntsa (A), Juyuintsa (B), and Sawastian (C).

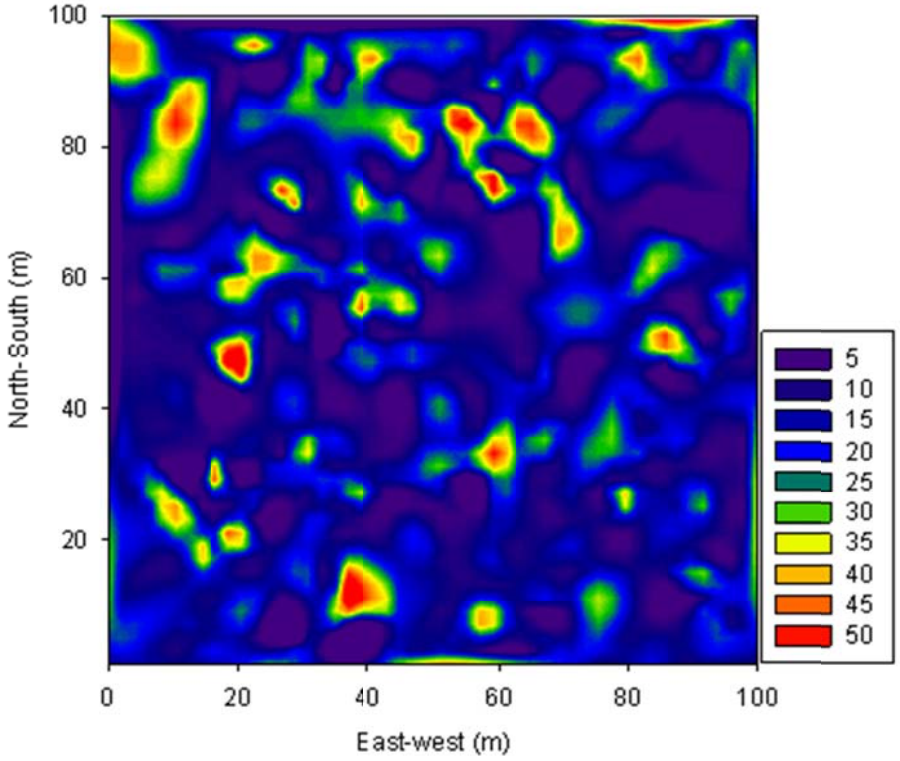
A.



B.


100
80
60
40
20
0
North-South (m)
0
20
40
60
80
100
East-West (m)
5
10
15
20
25
30
35
40
45

C.



Point-pattern analysis examines spatial aggregations, habitat associations, potential mechanisms that dictate diversity patterns, and forest dynamics. For instance, the short-distance clustering and the lack of repulsion between adult and juvenile ponderosa pines indicate patchy distribution and ongoing recruitment (Franklin and Santos 2011). In Sri Lanka, strong segregation and clustering patterns show that neutral theory was not supported (Wiegand et al. 2007a). The bivariate inhibition and clustering relationships at different distance lags between medium and large juniper trees in Idaho suggest a size-dependent distribution (Strand et al. 2007). The positive and negative spatial associations between plants in Chile are affected by the environment (Fajardo et al. 2008). Species distribution changes from random at local scale to clustering at broad scale. Negative association occurs between trees of different size classes, but positive

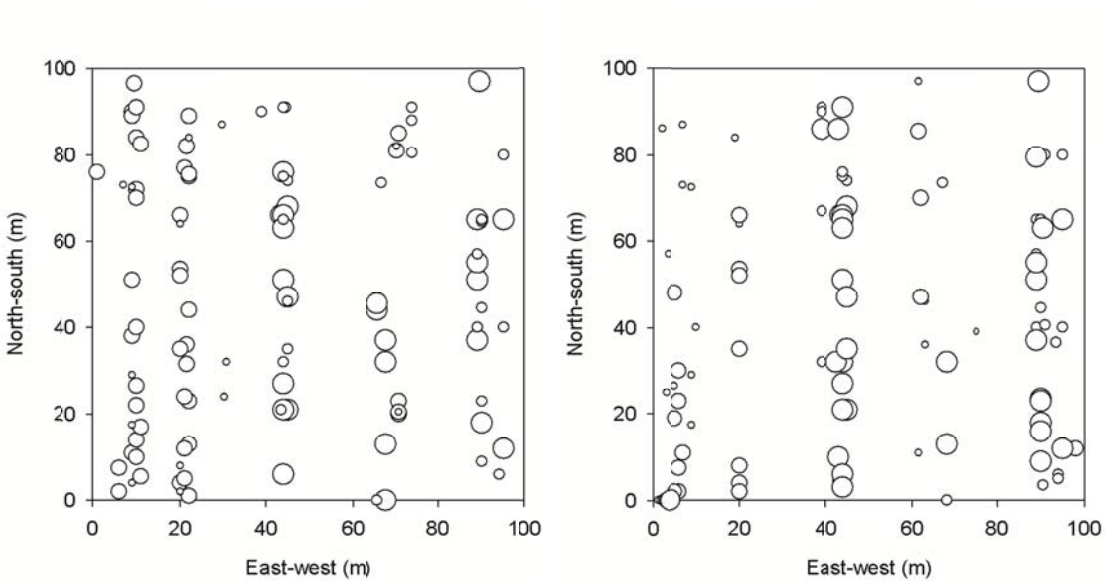
association is found between saplings and dead trees (Fajardo et al. 2008). A comparative study in Panama and Sri Lanka shows that at small scale local diversity is decreased by "repellers" in Panama and increased by "accumulators" in Sri Lanka. Balanced inter-species interactions may be characteristic of species-rich forests (Wiegand et al. 2007b). Spatial aggregation of trees and habitat associations with topography and light are observed in an Ecuadorian forest, although habitat partitioning does not explain the coexistence of related species (Valencia et al. 2004b).

As an exploratory analysis, this dissertation study examined local clustering patterns of trees in different sizes and between trees in varying heights. The univariate Local Indicators of Spatial Association (LISA) using tree DBH and height separately indicated the presence of significant clusters that showed clusters occurred in different parts of the three plots. In Yutsuntsa, tree cluster types based on DBH showed similar spatial distributions to tree clusters based on height. There was a high concentration of larger or taller trees (High-High clusters) on the central-eastern side of the plot (Figure 4.8A). Clusters of trees with small DBH or low height (Low-Low) were both concentrated on the western side of the plot. Smaller trees and their surrounding larger trees, as well as shorter trees and their surrounding taller trees (Low-High) were distributed across the entire plot (Figure 4.8A). In Juyuintsa, the spatial correspondence between distributions of clusters based on DBH vs. based on height was less obvious than Yutsuntsa. The High-High clusters of trees with greater DBH and height both occurred on the southern side of the plot, but clusters of tall trees were more prominent (Figure 4.8B). Low-Low clusters of trees with smaller DBH and low height occurred on the northern part, but shorter trees showed greater presence (Figure 4.8B). There were only a few High-Low or Low-High clusters of DBH or height in the central part of the plot. In contrast, visual inspections could not detect spatial correspondence between clusters for

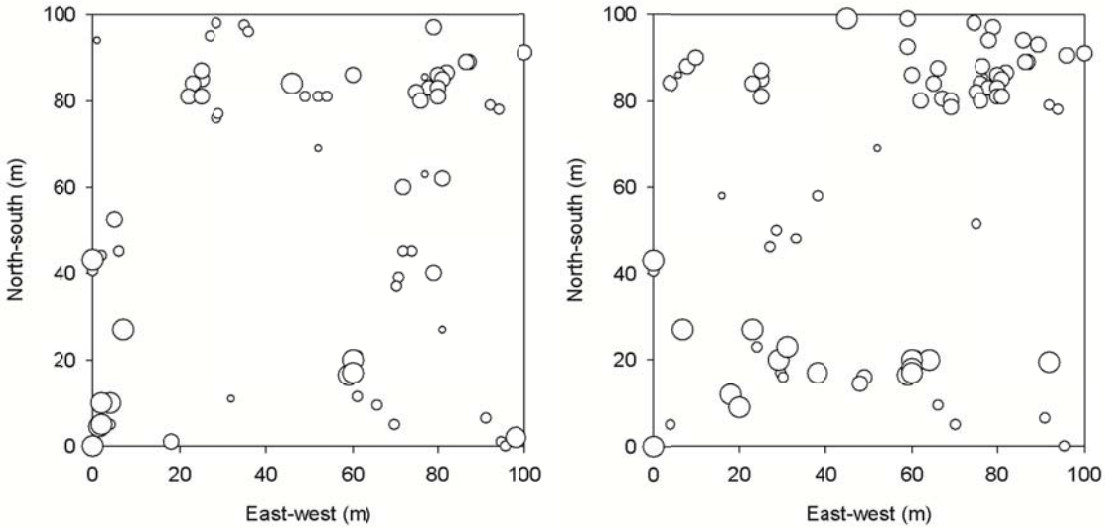
DBH and for height in Sawastian. For example, taller trees that were surrounded by other taller trees occurred on the northwestern part of the plot but only a few High-High clusters for DBH were there (Figure 4.8C). Likewise, on the western side where shorter trees that occurred with other shorter trees, there were no Low-Low clusters for DBH. Some spatial correspondence of High-High clusters appeared near the southern side of the plot, but there were more clusters for DBH than for height (Figure 4.8C).

Figure 4.8. Distribution of significant ($p < 0.05$) spatial clusters of DBH (left) and height (right) values in A) Yutsuntsa, B) Juyuintsa, and C) Sawastian. Bubble size from the largest to the smallest represents clusters of High-High, Low-Low, Low-High, and High-Low (see text for cluster definition), respectively.

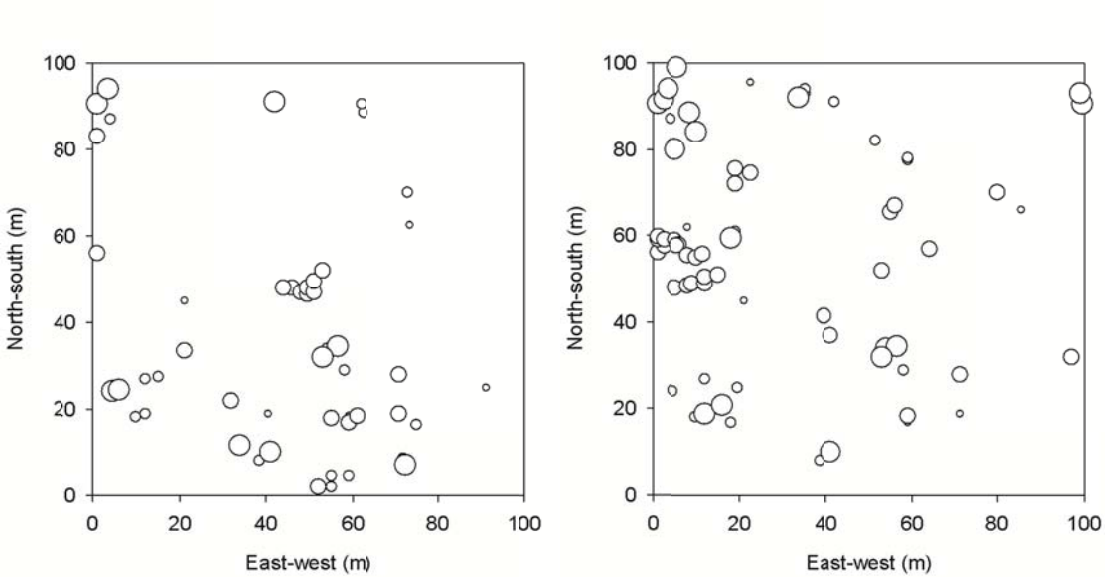
A.



B.


North-south (m)
East-west (m)
0
20
40
60
80
100

C.


North-south (m)
East-west (m)
0
20
40
60
80
100

The degree of spatial correspondence between the distribution of tree DBH and height clusters varied among the three plots. It is possible that such pattern rises from spatial heterogeneity in forest gap dynamics or forest turnover. In Yutsuntsa, the corresponded High-High and Low-Low clusters for DBH vs. height did not overlap much within the plot, suggesting a gradient of potential forest turnover may be present and this gradient divides trees into distinctive size (or age) groups. The less obvious spatial correspondence in Juyuintsa indicated that some clustered taller/shorter trees did not overlap in areas where clustering of some larger/smaller trees occurred. Therefore, Juyuintsa may represent a forest mixed with trees in different growth and successional stages. In Sawastian, the sites where clusters of tree DBH occurred did not correspond well to the locations of clusters for tree height. The lack of correspondence between two types of spatial associations (clusters for DBH vs. clusters for height) may reflect the complexity of former disturbance regimes in Sawastian. Future research should further compare the examinations of spatial associations between DBH vs. DBH, height vs. height, and DBH vs. height among the three plots (Anselin 1995, Anselin et al. 2002). Difference in spatial associations between large vs. tall trees (High-High clusters), small vs. short trees (Low-Low), small vs. tall trees (Low-High), and large vs. short trees (High-Low) may reveal the heterogeneity of forest dynamics in more detail. Furthermore, the bivariate associations examined in this dissertation and in a future study should look into how life history traits of different species, such as shade tolerance or dispersal mode, may play a role in affecting the spatial associations.

In addition, given the great species richness within each tree size class in the study area, interactions between dominant trees in different families, genera, and species may be important in governing spatial distributions and neighborhood associations. A preliminary examination of the bivariate relationship between trees in Arecaceae vs.

Moraceae in Yutsuntsa showed that attraction occurred at low (< 5 m) and intermediate (20-35 m) distance ranges. These families showed repulsion between each other at intermediate-low (5-20 m) and long (> 35 m) distances. The relationships may be associated with the ecological or spatial relationships between Arecaceae vs. Moraceae, as well as habitat characteristics interacting with the occurrence of these families. At the species level, dominant *Oenocarpus bataua* and *Virola flexuosa* were respectively denser at the northeastern and southwestern corners in the Yutsuntsa plot (Figure 4.9). *Oenocarpus bataua* and *Iriartea deltoidea* showed higher density on the western side of Juyuintsa plot (Figure 4.10). Spatial clustering or attraction/repulsion between species may occur in areas where these species are abundant. A future examination of the spatial relationships between dominant species/genera in different size or height classes may shed light on ecological interactions, such as interspecific competition or non-competitive coexistence that was not examined in this dissertation.

Figure 4.9. Density (number of individuals in each 20 X 20 m grid) in the interpolated surface for *Oenocarpus bataua* (top) and *Virola flexuosa* (bottom) in Yutsuntsa.

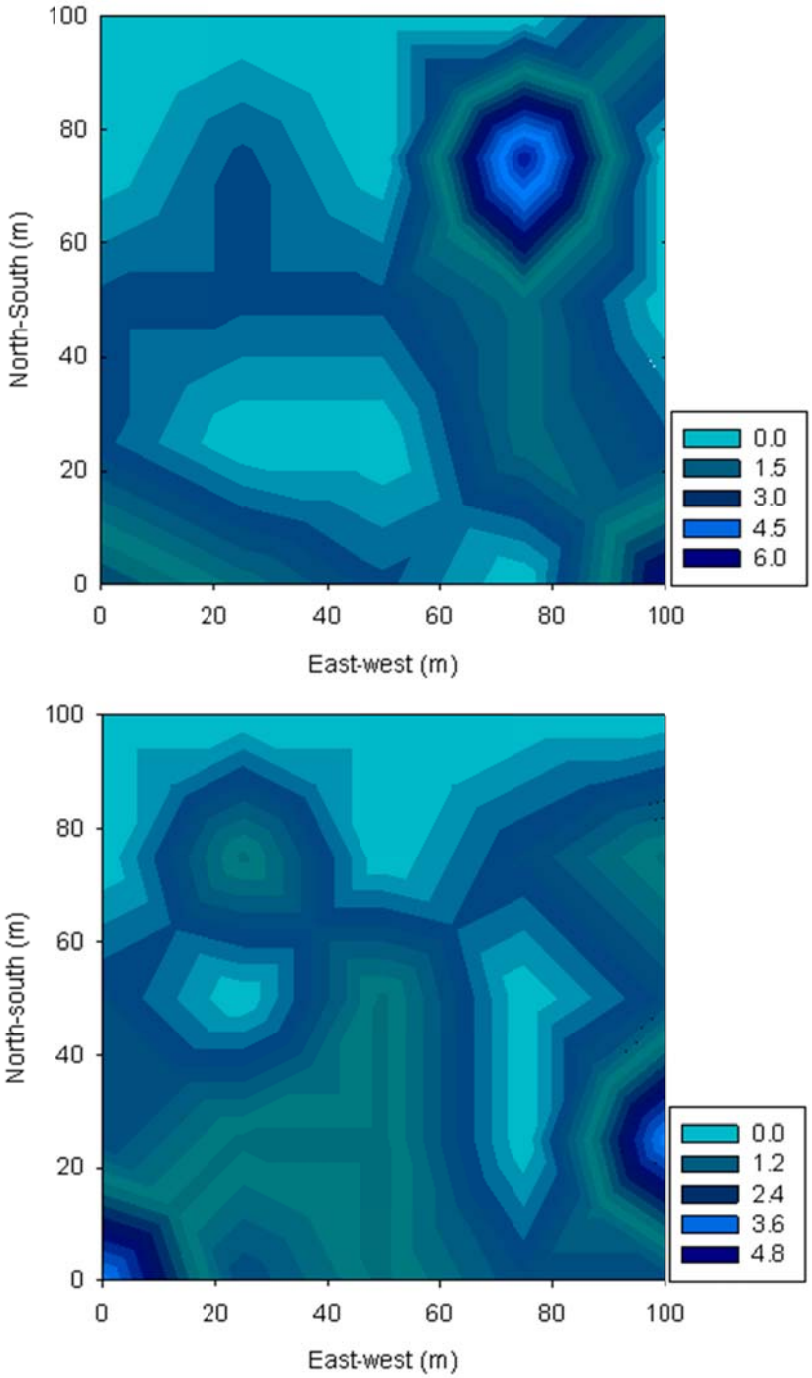
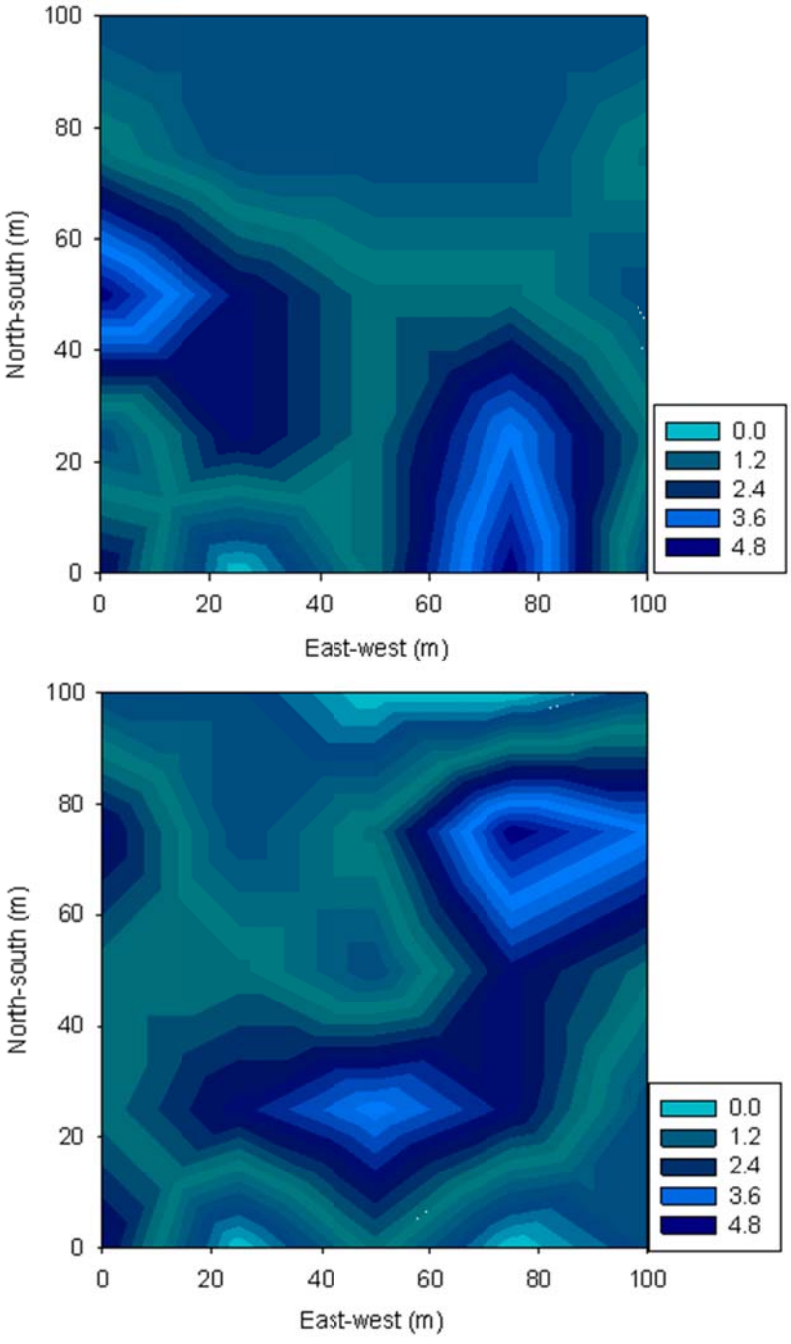


Figure 4.10. Density (number of individuals in each 20 X 20 m grid) in the interpolated surface for *Oenocarpus bataua* (top) and *Iriartea deltoidea* (bottom) in Juyuintsa.



Scale dependence in spatial point pattern and neighborhood analysis may affect how spatial clustering vs. dispersion and attraction vs. repulsion is defined. A calculation of the local version of Ripley's K (proposed by Getis and Franklin 1987) for trees in Yutsuntsa was used to describe an overall spatial pattern at a particular distance (Appendix B). There was a gradient in spatial distribution patterns and a shift in clustered vs. dispersed areas in Yutsuntsa. At distance = 10 m, trees with a clustered distribution were located from the northern through central to the southern sides of the plot as a continuous belt of clustering. The southeastern corner of the plot also showed a clustered distribution. At distance = 15 m, the clustered belt remained whereas the southeastern corner began to show dispersion. The dispersion at the southeastern corner expanded at distance = 20 m and 25 m, dividing the plot into two discrete areas of clustering vs. dispersion (Appendix B). The non-changing area of clustering tree distribution suggested that more than half of the plot showed strong clustering under a great range of neighborhood size. The dispersion that increased with increasing neighborhood size indicated the complexity of examining tree distribution and how "scale" of examination (e.g. the neighborhood size) may affect the interpretation of the local tree distribution. Studying "multiple scales of clustering" of spatial patterns at a particular distance or a spatial point at multiple distances should be the goal of future research (Wiegand et al. 2007c).

Chapter 5: Beta diversity among one-ha plots in eastern Ecuador and northern Peru

RESULTS

The analyses were conducted with two sets of plot data: 49 one-ha plots and a subset that included 37 one-ha plots that were located in non-flooded ("terra firme") forests after eliminating plots that contained indicative species of floodable or swamp forests.

Species composition and diversity

The beta diversity study in this dissertation chapter was primarily focused on between-plot floristic variation at the regional scale at which a broader spatial extent of understanding of biodiversity patterns in conservation biogeography was embedded. The tree species inventory data in northeastern Ecuador, southeastern Ecuador, and Loreto, Peru contained multiple individuals of morphospecies that were not identified to species level. It was not possible to distinguish among the morphospecies of the same genus or family without comparing the herbarium vouchers. Therefore, I eliminated all morphospecies in the 49 plots in order to avoid underestimating or overestimating between-plot species diversity. As a result, the plot data in the analysis included 1132, 347, and 966 species in northeastern Ecuador, southeastern Ecuador, and Loreto, Peru, respectively, or a total of 1745 species for all 49 plots. The subset plot data included 1039, 347, and 953 species in northeastern Ecuador, southeastern Ecuador, and Loreto, Peru, respectively, or a total of 1660 species. Plots in Loreto, Peru had the highest Fisher's alpha, Shannon-Wiener, and Simpson's inverse diversity indices whereas plots in southeastern Ecuador showed the lowest (Table 5.1).

Table 5.1. Abundance and species diversity indices of plots in each of the three study regions and all 49 plots together (A), and of the subset plots (B).

A.

	Northeastern Ecuador	Southeastern Ecuador	Loreto, Peru	All 49 plots
Number of plots	34	3	12	49
Number of species	1132	347	966	1745
Number of individuals	19798	1305	6535	27823
Fisher's alpha diversity index	219.36	100.02	225.66	332.55
Shannon-Wiener diversity index	5.8	4.74	5.82	6.16
Simpson's inverse diversity index	101.88	46.47	176.66	151.77

B.

	Northeastern Ecuador	Southeastern Ecuador	Loreto, Peru	All 37 plots
Number of plots	23	3	11	37
Number of species	1039	347	953	1660
Number of individuals	13573	1305	5987	20865
Fisher's alpha diversity index	261.92	100.02	319.06	423.83
Shannon-Wiener diversity index	5.9	4.74	6.03	6.31
Simpson's inverse diversity index	117.68	46.47	215.3	185.02

Plots in the three regions shared a great number of dominant families and genera. A list of the ten most abundant families in the three regions all contained the same seven families. Plots in northeastern and southeastern Ecuador shared at least one additional

abundant family in common whereas plots in southeastern Ecuador and Loreto shared one additional family (Table 5.2). At the genus level, a list of the ten most abundant genera in the three regions all contained the same two genera. Plots in northeastern and southeastern Ecuador shared four additional abundant genera in common whereas plots in northeastern Ecuador and Loreto shared at least one additional family (Table 5.2). Arecaceae (the palm family) had relative percentage abundance > 10% in Ecuador, but the relative percentage abundance dropped to 5% in Peru (Table 5.2). Likewise, the most abundant genus in northeastern Ecuador and the second most abundant genus in southeastern Ecuador were both in the palm family, but genus in the palm family was only ranked as the tenth most abundant genus in Peru. *Iriartea* in northeastern Ecuador accounted for 7% of total tree individuals; *Oenocarpus* and *Iriartea* in the plots in southeastern Ecuador accounted for 10.8% of the total tree abundance. In contrast, *Astrocaryum* in Loreto only accounted for 2% of total tree individuals (Table 5.2).

Similarly, the Ecuadorian plots harbored much greater abundance of palm species than the Peruvian plots. The two top abundant species in southeastern Ecuador were palms. These palm species accounted for 10.8% of total abundance in southeastern Ecuador (Table 5.2). Only one palm species was among the top five most abundant tree species in northern Peru and it only accounted for < 2% of total tree abundance (Table 5.2). *Iriartea deltoidea* was a palm species that occurred in plots in both Ecuadorian regions, but its relative abundance in northeastern Ecuador was higher than in southeastern Ecuador (Table 5.2). *Eschweilera coriacea* was a shared and abundant species between the Ecuadorian and the Peruvian plots, with similar relative abundances (Table 5.2).

Percentages of abundant tree families did not differ much among the plots in the three regions, however, relative abundances of the top tree genera in Loreto showed

lower percentages than in the Ecuadorian plots (Table 5.2). Such a pattern became more pronounced at the species level, when the most abundant tree species in Loreto only accounted for around or less than 2% of total abundance whereas the most abundant tree species in northeastern and southeastern Ecuador accounted for around or over 7% of total abundance (Table 5.2).

Table 5.2. The most abundant families, genera, and species and their percentage abundances in 49 plots (A) and 37 plots (B) in northeastern Ecuador, southeastern Ecuador, and Loreto, Peru.

A.

Northeastern Ecuador	Southeastern Ecuador	Loreto, Peru
Abundant family *(%)*		
Arecaceae (17.71)	Arecaceae (11.64)	Fabaceae (14.73)
Fabaceae (12.06)	Bombacoideae withinin Malvaceae (11.12)	Myristicaceae (11.19)
Lecythidaceae (5.5)	Meliaceae (7.73)	Sapotaceae (5.82)
Moraceae (5.42)	Myristicaceae (7.35)	Euphorbiaceae (5.65)
Myristicaceae (5.02)	Moraceae (5.59)	Lecythidaceae (5.34)
Euphorbiaceae (4.73)	Lecythidaceae (5.28)	Moraceae (5.32)
Bombacoideae within Malvaceae (4.11)	Fabaceae (4.67)	Arecaceae (4.91)
Meliaceae (3.9)	Sapotaceae (4.06)	Burseraceae (3.71)
Annonaceae (3.84)	Lauraceae (3.98)	Chrysobalanaceae (3.54)
Sapotaceae (3.58)	Euphorbiaceae (3.83)	Lauraceae (3.44)
Abundant genus *(%)*		
Iriartea (7.29)	*Matisia (9.42)*	*Eschweilera (5.05)*
Inga (3.95)	*Oenocarpus (5.82)*	*Virola (4.13)*
Eschweilera (3.36)	*Iriartea (4.98)*	*Iryanthera (4.03)*
Matisia (2.92)	*Guarea (4.21)*	*Pouteria (3.31)*
Virola (2.88)	*Eschweilera (4.06)*	*Macrolobium (3.13)*
Guarea (2.41)	*Virola (4.06)*	*Tachigali (3.06)*
Pouteria (2.29)	*Inga (3.14)*	*Protium (3.02)*

(Table 5.2 continued)

Euterpe (1.95)	*Trichilia (2.91)*	*Licania (2.68)*
Mauritiella (1.9)	*Iryanthera (2.53)*	*Otoba (2.49)*
Protium (1.84)	*Protium (1.91)*	*Astrocaryum (2.02)*
Abundant species (%)		
Iriartea deltoidea (7.29)	*Matisia lasiocalyx* (8.12)	*Eschweilera coriacea* (2.04)
Euterpe precatoria (1.95)	*Oenocarpus bataua* (5.82)	*Astrocaryum murumuru* (1.96)
Mauritiella armata (1.9)	*Iriartea deltoidea* (4.98)	*Macrolobium microcalyx* (1.43)
Mauritia flexuosa (1.8)	*Eschweilera coriacea* (3.29)	*Virola calophylla* (1.4)
Matisia malacocalyx (1.43)	*Iryanthera macrophylla* (1.84)	*Micrandra elata* (1.35)

B.

Northeastern Ecuador	Southeastern Ecuador	Loreto, Peru
Abundant family *(%)*		
Fabaceae (11.42)	Arecaceae (11.64)	Fabaceae (13.18)
Arecaceae (10.56)	Bombacoideae withinin Malvaceae (11.12)	Myristicaceae (12.16)
Moraceae (6.65)	Meliaceae (7.73)	Moraceae (5.53)
Lecythidaceae (6.24)	Myristicaceae (7.35)	Euphorbiaceae (5.51)
Myristicaceae (5.61)	Moraceae (5.59)	Arecaceae (5.34)
Bombacoideae within Malvaceae (5.34)	Lecythidaceae (5.28)	Sapotaceae (5.18)
Euphorbiaceae (4.78)	Fabaceae (4.67)	Lecythidaceae (4.79)
Meliaceae (4.69)	Sapotaceae (4.06)	Burseraceae (4.08)
Lauraceae (3.87)	Lauraceae (3.98)	Lauraceae (3.67)
Cecropiaceae (3.68)	Euphorbiaceae (3.83)	Annonaceae (3.51)

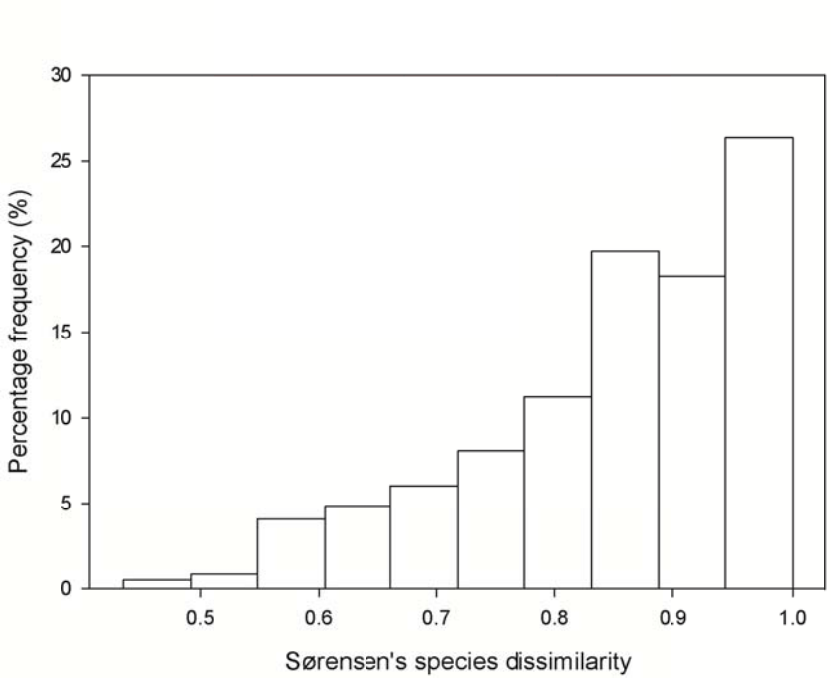
(Table 5.2 continued)

Abundant genus *(%)*		
Iriartea (6.84)	*Matisia* (9.42)	*Eschweilera* (4.48)
Inga (4.35)	*Oenocarpus* (5.82)	*Iryanthera* (4.43)
Matisia (4)	*Iriartea* (4.98)	*Virola* (4.41)
Eschweilera (3.78)	*Guarea* (4.21)	*Protium* (3.32)
Guarea (2.87)	*Eschweilera* (4.06)	*Macrolobium* (3.12)
Virola (2.81)	*Virola* (4.06)	*Otoba* (2.74)
Protium (2.39)	*Inga* (3.14)	*Tachigali* (2.71)
Pourouma (2.77)	*Trichilia* (2.91)	*Pouteria* (2.51)
Rinorea (2.08)	*Iryanthera* (2.53)	*Licania* (2.41)
Pouteria (2.05)	*Protium* (1.91)	*Astrocaryum* (2.22)
Abundant species (%)		
Iriartea deltoidea (6.84)	*Matisia lasiocalyx* (8.12)	*Micrandra elata* (1.49)
Matisia malacocalyx (2.03)	*Oenocarpus bataua* (5.82)	*Rinorea apiculata* (1.29)
Rinorea apiculata (1.64)	*Iriartea deltoidea* (4.98)	*Astrocaryum murumuru* (0.84)
Eschweilera coriacea (1.61)	*Eschweilera coriacea* (3.29)	*Tachigali tessmannii* (0.8)
Brownea grandiceps (1.43)	*Iryanthera macrophylla* (1.84)	*Macrolobium microcalyx* (0.75)

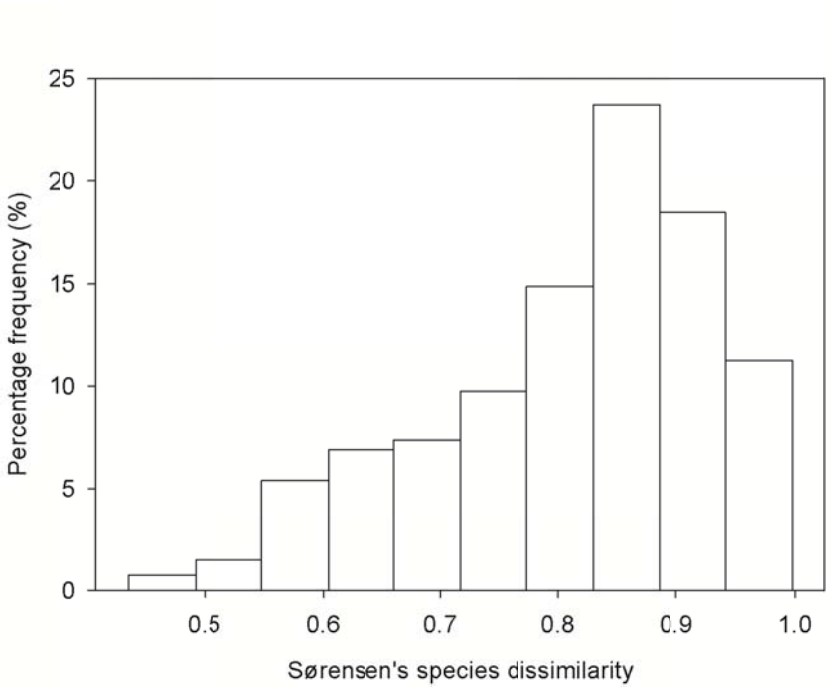
Although plots in these three regions shared some dominant families, genera, and species, paired plots differed greatly in their species and genus composition. At the species level, Sørensen's dissimilarity distance matrix for species abundance showed that on average 85% of the species composition differed between paired plots. The paired plots showed 44%-100% of dissimilarity in species composition, but over 75% of the paired plots had Sørensen's species dissimilarity indices > 0.8 (Figure 5.1A). Similarly, the paired plots from the subset data had 44%-100% of dissimilarity in species composition, and over 67% of the paired plots had Sørensen's species dissimilarity indices > 0.8 (Figure 5.1B). At the genus level, Sørensen's dissimilarity distance matrix for genus abundance indicated that on average 67% of the genus composition differed between paired plots. The paired plots showed 32%-96% of dissimilarity in genus composition, but only 29% of the paired plots had Sørensen's species dissimilarity index > 0.8 (Figure 5.1C). In particular, paired plots between the two regions in Ecuador differed in 44%-100% of species composition (mean dissimilarity = 0.81 ± 0.005), plots between southeastern Ecuador and Loreto were different in 52%-100% of species composition (mean dissimilarity = 0.87 ± 0.01), and plots between northeastern Ecuador and Loreto had 44%-100% difference in species composition (mean dissimilarity = 0.84 ± 0.003).

Figure 5.1. Percentage frequency distribution of Sørensen's dissimilarity index at the species level (A), species level using the subset data (B), and genus level (C).

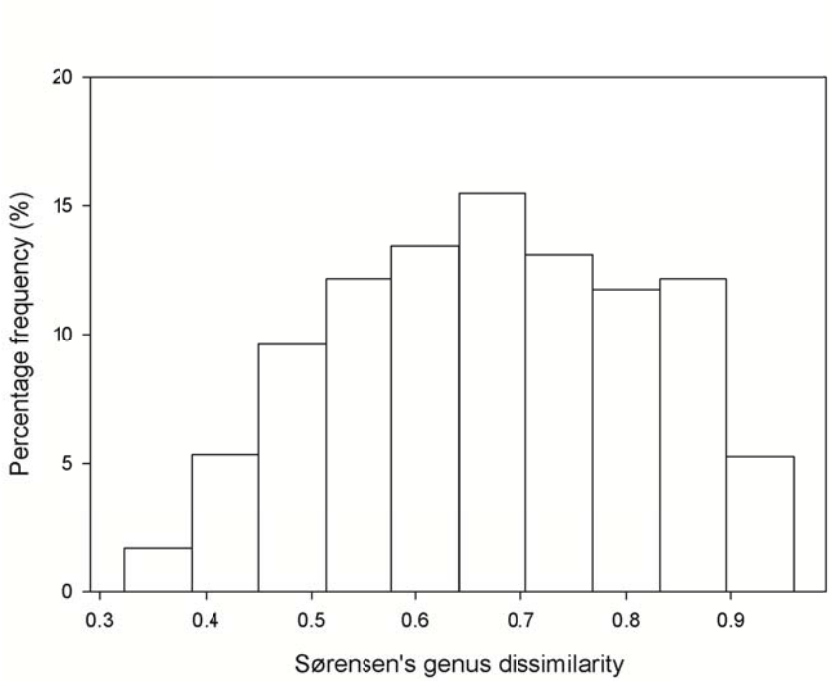
A.



B.


Percentage frequency (%)
25
20
15
10
5
0
0.5
0.6
0.7
0.8
0.9
1.0
Sørensen's species dissimilarity

C.

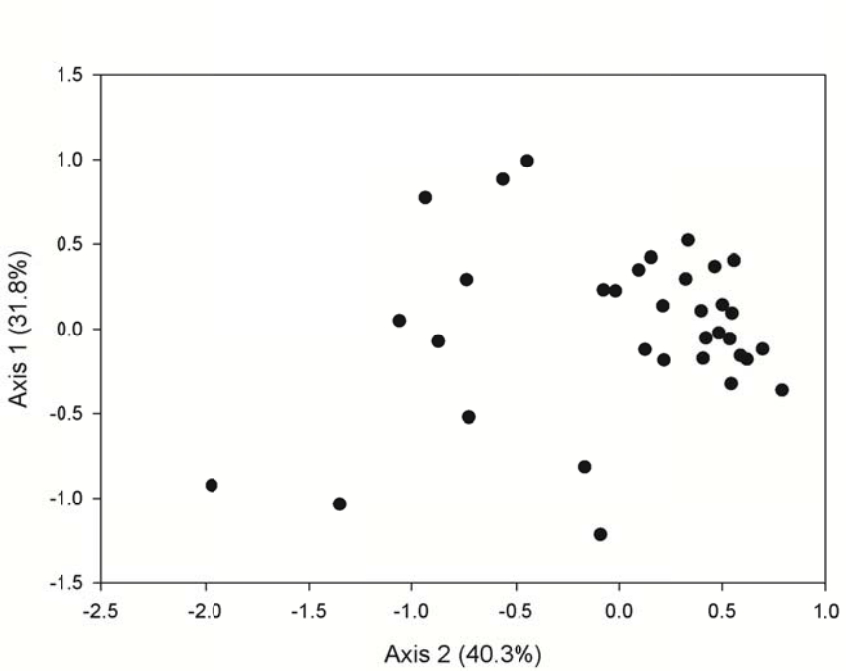

Percentage frequency (%)
20
15
10
5
0
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Sørensen's genus dissimilarity

Ordination among one-ha plots

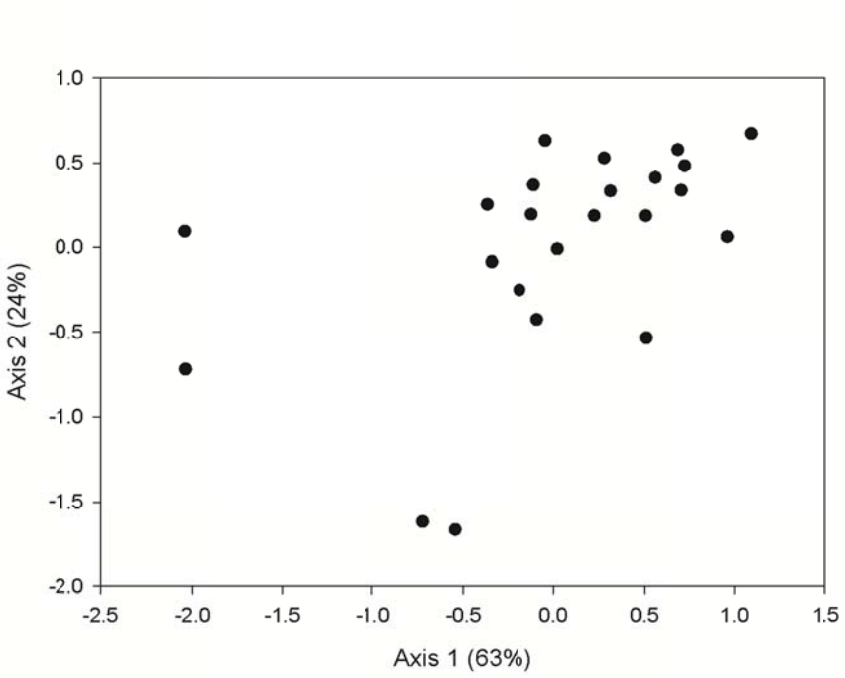
The examination of potential species assemblages at the beta diversity level took place by comparing ordination patterns among plots in northeastern Ecuador and northern Peru. Ordination analysis was conducted in order to examine whether or not the plots formed clusters in ordination space along geographic or environmental gradients. The Non-metric Multidimensional Scaling (NMS) ordination (using Sørensen's similarity distance matrix based on species abundance) suggested that plots within northeastern Ecuador or Peru showed varying similarity with one another in ordination space. Overall, for the ordinations in northeastern Ecuador and Peru, three-dimensional axes explained 92% (stress = 7.68, instability = 0.0003, $p < 0.05$) and 88% (stress = 3.18, instability = 0.0003, $p < 0.05$) of the data variance. Two-dimensional axes explained 87% (stress = 10.37, instability = 0.0002, $p < 0.05$) and 81.8% (stress = 4.97, instability = 0.0003, $p < 0.05$) of the data variance for the subset plots in northeastern Ecuador and Peru. Visual inspection of the ordination axes suggested that although plots in northeastern Ecuador formed a distinctive cluster, spatial distribution of the plots in ordination space did not correspond to the geographic locations of these plots (Figure 5.2A, B). Four plots that were not part of the ordination cluster in Figure 5.2B were Parche, Yarina, Teresita, and Zancudo. Likewise, the spatial distribution of the Peruvian plots in ordination space did not correspond to the plots' geographic locations (Figure 5.2C, D).

Figure 5.2. NMS ordination scores of the two axes explaining the highest percentage variance of the data in northeastern Ecuador (A), subset in northeastern Ecuador (B), Loreto, Peru (C), and subset in Loreto (D). Each point represents a plot. Value in the parenthesis indicates the percentage variance explained by the axis.

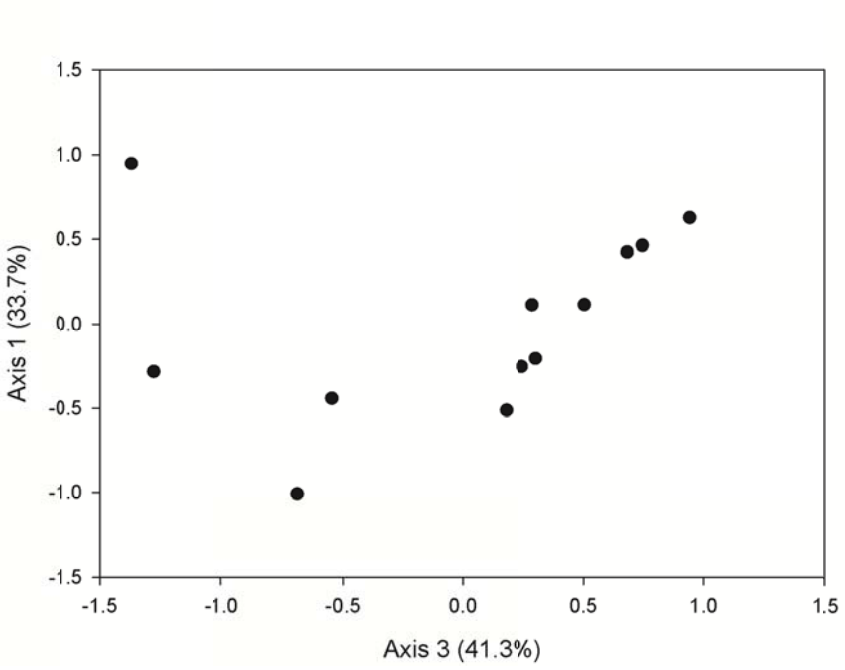
A.



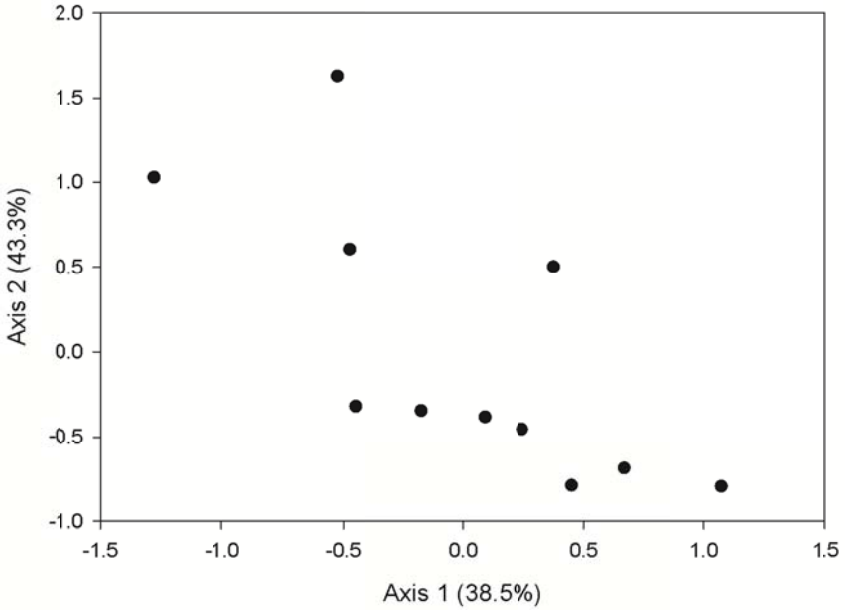
B.


1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
Axis 2 (24%)
-2.5
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
Axis 1 (63%)

C.


1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
Axis 1 (33.7%)
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
Axis 3 (41.3%)

D.

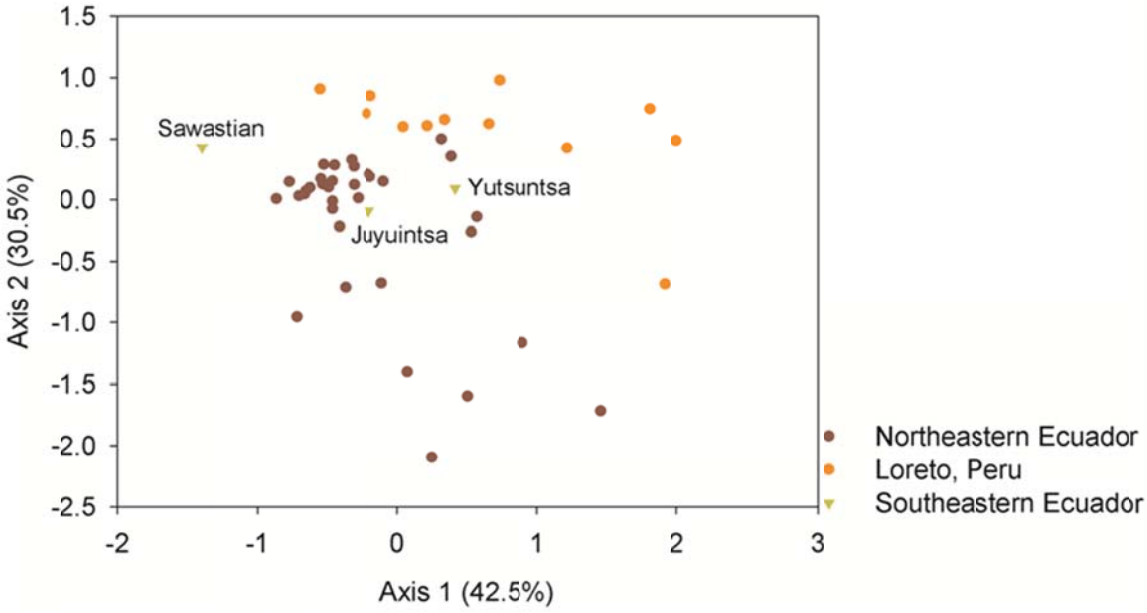


At a larger regional scale, the NMS ordination for all 49 plots in western Amazon revealed a cluster in Ecuador. With 73% of the data variance explained by the two-dimensional axes (stress = 15.6, instability = 0.0004, $p < 0.05$), the ordination showed a cluster of most of the northeastern Ecuadorian plots (Figure 5.3A). A similar pattern occurred when the subset plots were used, where 74% of the data variance was explained by the two-dimensional axes (stress = 11.27, instability = 0.00007, $p < 0.05$), except for the four plots in northeastern Ecuador that were outliers in ordination space (Figure 5.3B). Plots in southeastern Ecuador had shorter ordination distances to plots in northeastern Ecuador than Peru. Plots in Peru were not clustered in ordination space, but formed a group that was distinguishable from the Ecuadorian plots (Figure 5.3A). Ordination distance between the Ecuadorian vs. Peruvian plots increased when the subset was used, forming more distinguishable groups between plots on the western

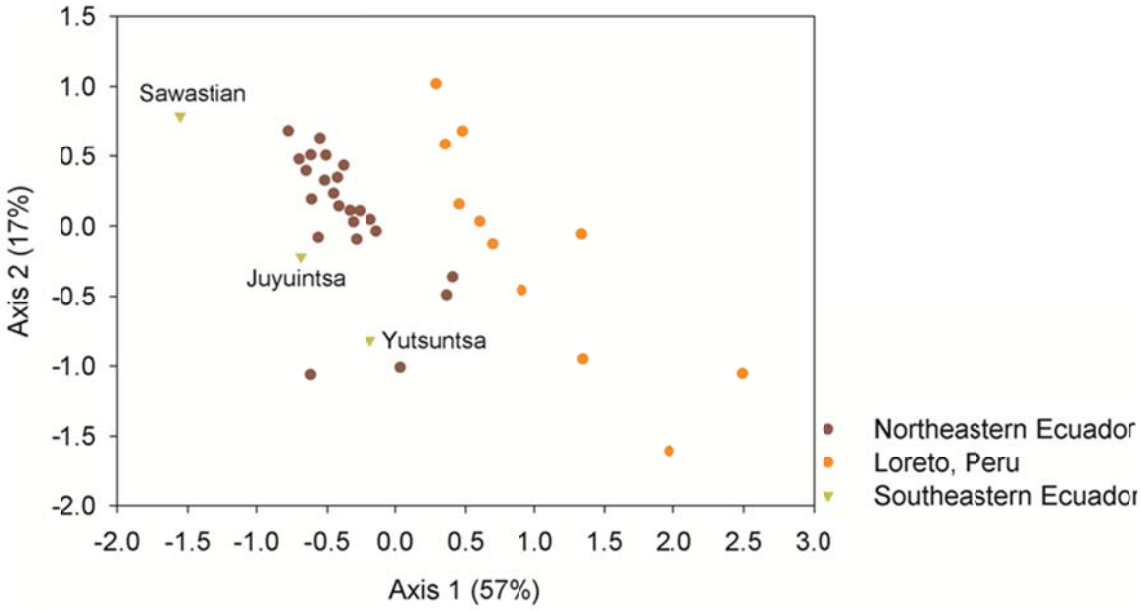
(Ecuadorian) vs. eastern (Peruvian) side of the study region (Figure 5.3B). Spatial distribution of the 49 plots and the 37 subset plots along ordination axes corresponded to the relative geographic locations of plots in Ecuador vs. Peru, but not for plots in northern vs. southern Ecuador.

Figure 5.3. NMS ordination scores of the two axes explaining the highest percentage variance of the data in all 49 plots (A) and in 37 subset plots (B) in western Amazon. Each point represents a plot. Value in the parenthesis indicates the percentage variance explained by the axis.

A.

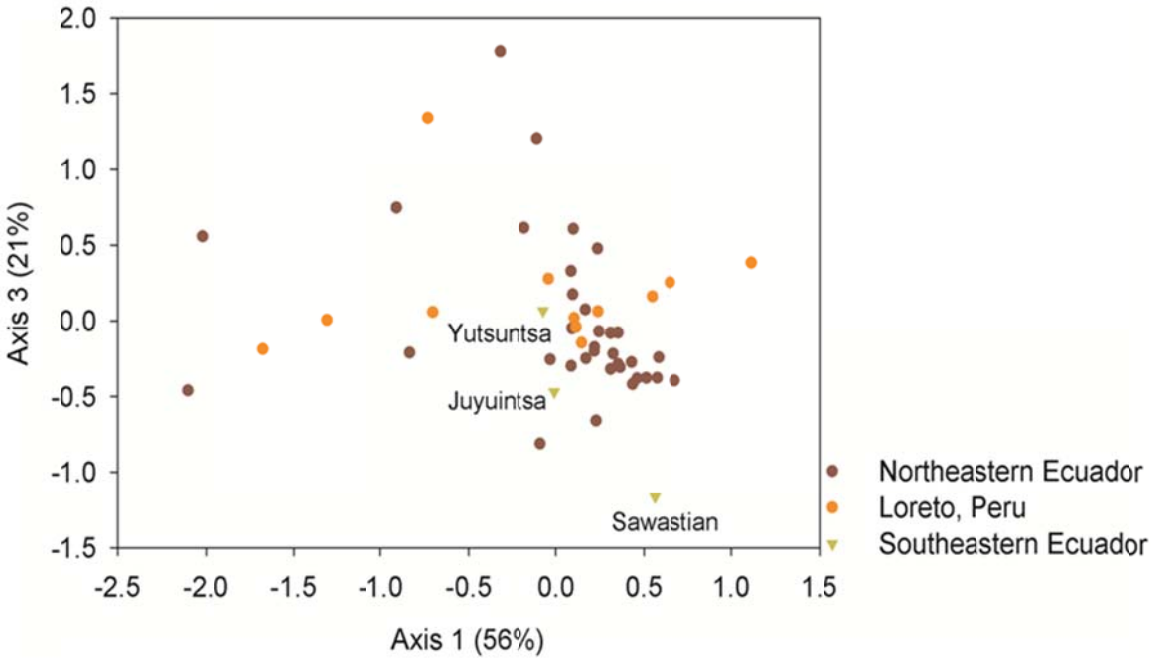


B.



The NMS ordination at the genus level revealed patterns similar to the species level. Plots in northeastern Ecuador formed a spatial cluster in the two-dimensional space (89% of data variance explained, stress = 12.3, instability = 0.0004, $p < 0.05$), but the spatial clustering did not correspond to the plots' geographic distribution. Plots in Peru showed neither ordinational clustering nor correspondence to their geographic locations (92% of data variance explained, stress = 4.17, instability = 0.0005, $p < 0.05$). The ordination of all 49 western Amazonian plots indicated that most plots in Ecuador formed a cluster in ordination space (91% of data variance explained in the three-dimensional space, stress = 9.61, instability = 0.0005, $p < 0.05$), but plots in Peru showed a dispersed distribution (Figure 5.4). Similar to the pattern observed at the species level, the plot distribution in ordination space showed slight correspondence to the relative geographic distribution of plots in northeastern Ecuador vs. northern Peru, but not for plots in northern vs. southern Ecuador.

Figure 5.4. NMS ordination scores of the two axes explaining the highest percentage variance of the data in all 49 plots at the genus level in western Amazon. Each point represents a plot. Value in the parenthesis indicates the percentage variance explained by the axis.



Kendall's Tau correlations between the ordination axes and individual species/genus suggested that many of the species/genera that showed the strongest correlations were among the most abundant families in the Amazonian plots, such as *Pouteria tenuipetiole* and *Pouteria cuspidata* ssp. *robusta* cf. in Sapotaceae, *Matisia obliquifolia* in Bombacoideae within Malvaceae, *Macrolobium bifolium* in Fabaceae, *Astrocaryum murumuru* and *Oenocarpus bataua* in Arecaceae, *Couroupita* in Lecythidaceae, and *Otoba* in Myristicaceae (Table 5.3A, B). Among all 71 environmental variables, precipitation in January, February, and July had the strongest correlations with the ordination axes for all 49 plots at both species and genus levels (Kendall's Tau ranging from -0.49 to 0.53), indicating an important role that

precipitation potentially plays in determining species composition (Table 5.3A). Precipitation in June and mean temperature of the wettest quarter had the strongest correlations with the ordination axes for 37 subset plots at a species level (Table 5.3B). This finding showed consistency with Gentry's finding (1988) that species richness and composition in lowland Neotropical forests are tightly correlated with precipitation.

Table 5.3. Kendall's Tau correlations between the ordination axes vs. individual species and the environmental variables using all plot data (A) and using subset of plot data (B). Only the highest/lowest Tau value is shown.

A.

Plots	Species/genus with the lowest Tau	Species/genus with the highest Tau
Species level		
Northeastern Ecuador	*Pouteria tenuipetiole* (-0.55)	*Matisia obliquifolia* (0.73)
Loreto, Peru	*Macrolobium bifolium* (-0.88)	*Astrocaryum murumuru* (0.81)
All 49 plots	*Spondias mombin* (-0.568)	*Licania hypoleuca* (0.48)
Genus level		
Northeastern Ecuador	*Couroupita* (-0.5)	*Tetrathylacium* (0.56)
Loreto, Peru	*Theobroma* (-0.81)	*Diospyros* (0.74)
All 49 plots	*Roucheri* (-0.54)	*Sapium* (0.51)
	Environmental variable with the lowest Tau	Environmental variable with the highest Tau
All 49 plots (species level)	Precipitation of July (-0.49)	Precipitation of January (0.53)
All 49 plots (genus level)	Precipitation of February (-0.44)	Precipitation of July (0.44)

B.

Plots	Species with the lowest Tau	Species with the highest Tau

(Table 5.3 continued)

Northeastern Ecuador	*Pouteria cuspidata* ssp. *robusta* cf. (-0.59)	*Matisia obliquifolia* (0.83)
Loreto, Peru	*Astrocaryum murumuru* (-0.86)	*Macrolobium bifolium* (0.77)
37 plots	*Oenocarpus bataua* (-0.6)	*Astrocaryum murumuru* (0.65)
	Environmental variable with the lowest Tau	Environmental variable with the highest Tau
37 plots	Precipitation of June (-0.58)	Mean temperature of the wettest quarter (0.56)

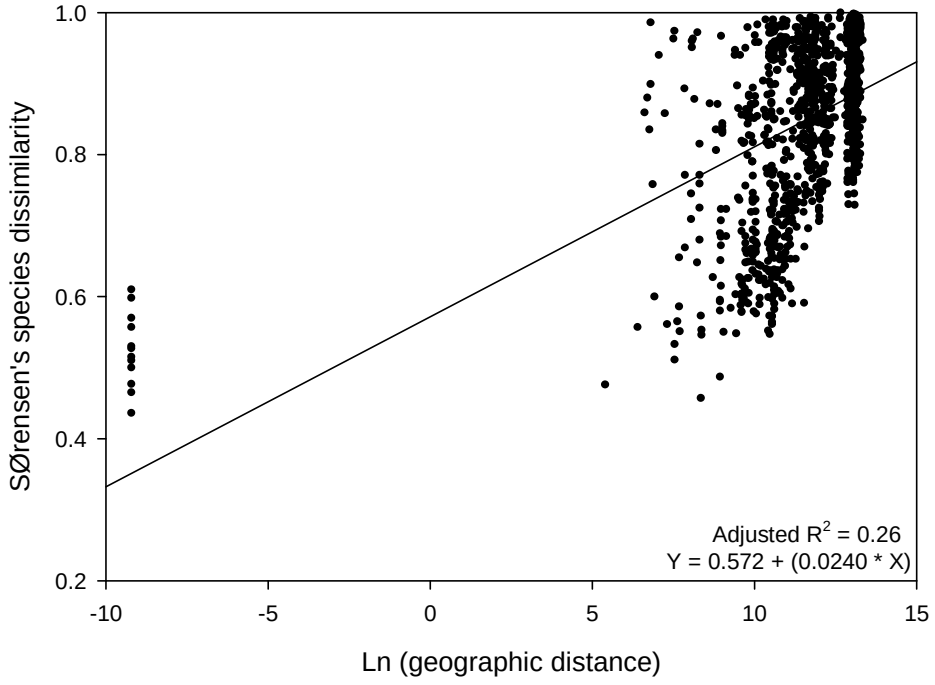
Mantel tests and indicator species analysis

In order to examine the extent to which floristic beta diversity patterns were associated with the heterogeneity of environmental attributes, Mantel tests were conducted for revealing whether or not the floristic composition was associated with geographic distances or with the biophysical environment. A positive trend appeared in the simple linear regression between pairwise Sørensen's species/genus dissimilarity index vs. pairwise Ln(geographic distance) between two plots (Figure 5.5). At both species and genus levels, the adjusted R^2 suggested minor correlations ($R^2 = 0.26$ at the species level and 0.13 at the genus level, $p < 0.001$). The Mantel test between Sørensen's species/genus dissimilarity distance matrix and the Euclidean distance matrix of Ln(geographic distance) showed a significant correlation (Mantel's $r = 0.51$, $p < 0.01$). When the subset of 37 plots was used for the Mantel test, a more significant correlation (Mantel's $r = 0.71$, $p < 0.01$) was found between Sørensen's species dissimilarity and Ln(geographic distance). Therefore, I used partial Mantel tests to examine the relationship between Sørensen's species/genus dissimilarity distance matrix

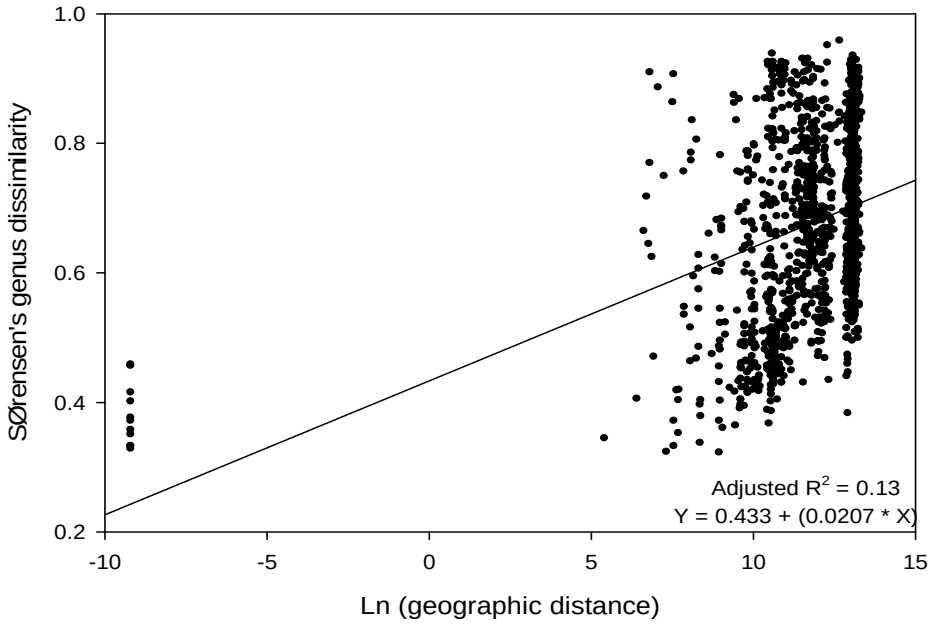
and the Euclidean distance matrix of each environmental variable while controlling the Euclidean distance matrix of Ln(geographic distance).

Figure 5.5. Linear regression between pairwise Ln(geographic distance) vs. Sørensen's species (A) and genus (B) dissimilarity index.

A.



B.



Despite the medium-low correlations between environmental variables and ordination axes (see above), there appeared to be congruence between the Euclidian distance matrices of bioclimatic variables and Sørensen's species/genus dissimilarity distance matrices using abundance data of all 49 plots. At the species level, 16 out of 19 bioclimatic variables obtained from WorldClim showed significant correlations with Sørensen's species dissimilarity distance matrices (partial Mantel correlation r = 0.16-0.3, $p < 0.05$). Annual range of temperature, mean temperature of the driest quarter, and precipitation of the wettest month were not significantly correlated with Sørensen's

species dissimilarity (partial Mantel correlation r = 0.1-0.16, $p > 0.05$). All monthly precipitations, except for the precipitation in April, were significantly correlated with Sørensen's species dissimilarity (partial Mantel correlation r = 0.11-0.27, $p < 0.05$). All monthly mean, maximum, and minimum temperatures were significantly correlated with Sørensen's species dissimilarity (partial Mantel correlation r = 0.17-0.28, $p < 0.05$). Elevation was the only topographic variable that showed a nearly significant correlation with Sørensen's species dissimilarity (partial Mantel correlation r = 0.14, p = 0.05). When the subset of 37 plots was used for the analysis, 18 out of 19 bioclimatic variables, one out of four topographic variables (elevation), eight out of 12 monthly precipitations, and all monthly mean, maximum, and minimum temperatures were significantly correlated with Sørensen's species dissimilarity (partial Mantel correlation r = 0.17-0.41, $p < 0.05$ or $p < 0.01$).

The partial Mantel correlations at the genus level had similar but less prominent patterns. Only 11 out of 19 bioclimatic variables obtained from WorldClim showed significant correlations with Sørensen's species dissimilarity distance matrices (partial Mantel correlation r = 0.12-0.23, $p < 0.05$). Isothermality, annual range of temperature, mean temperatures of the wettest and driest quarters, and precipitations of the wettest, warmest, and coldest quarters were not significantly correlated with Sørensen's species dissimilarity (partial Mantel correlation r = 0.12-0.16, $p > 0.05$). Elevation, aspect, slope, and compound topographic index (CTI) did not show significant correlations with Sørensen's species dissimilarity (partial Mantel correlation r = -0.07-0.09, $p > 0.05$).

Gentry (1988) suggested that tropical tree communities are predictable from environmental parameters. Beta diversity may be partially linked to the extent of faithfulness of certain species towards some environmental attributes. Therefore, I used indicator species analysis to identify multiple species in all 49 plots and in the 37 subset

plots that had a significant ($p < 0.1$ or $p < 0.05$) indicator value for higher, intermediate, or lower values of different environmental variables. I hereby only present the top ten indicator species/genera of the environmental variables that showed the strongest correlations with species/genus ordination axes in NMS or with Sørensen's species dissimilarity in the partial Mantel tests. *Roucheria punctata*, *Licania heteromorpha*, *Macrolobium limbatum*, *Helicostylis scabra*, and *Macrolobium bifolium* were indicators for low July and high January precipitations (Table 5.4A). In addition, different species of *Iryanthera* were also indicators of low July and high January precipitations. Another species of *Iryanthera* showed indication of mean diurnal range of temperature. Different species of *Perebea* were indicative of low maximum temperature of the warmest month and high January precipitation (Table 5.4A). One palm species, *Iriartea deltoidea*, was an indicator for low maximum temperature of the warmest month (Table 5.4A). With the subset data of 37 plots, *Gustavia longifolia*, *Siparuna* cf. *decipiens*, *Iriartea deltoidea*, *Matisia malacocalyx*, *Melicoccus novogranatensis*, and *Brownea grandiceps* were indicators of high precipitations of both the wettest and driest months (Table 5.4B). *Gustavia longifolia*, *Siparuna* cf. *decipiens*, *Iriartea deltoidea*, and *Matisia malacocalyx* were also indicative of high isothermality (Table 5.4B). *Protium subserratum* was an indicator of both low mean diurnal range of temperature and low isothermality. *Tetrathylacium macrophyllum* and *Grias neuberthii* showed indication of both high precipitation of the wettest month and high mean diurnal range of temperature (Table 5.4B).

Table 5.4. Results of indicator species analysis (based on species abundance) for associations with environmental variables using data of 49 plots (A) and subset data of 37 plots (B). Only top ten species with the lowest *p* value and then the highest indicator value for each variable are listed.* = $p < 0.1$, ** = $p < 0.05$, *** = $p < 0.01$. H, I, or L represent higher (H), intermediate (I), or lower (L) value of the environmental variable.

A.

Environmental variable	Species	Indicator value	Environmental variable value
Precipitation of July	*Virola calophylla*	61.2**	L
	Coccoloba cf. fallax	50**	H
	Roucheria punctata	50**	L
	Byrsonima putumayensis	49.6**	I
	Licania heteromorpha	48.9**	L
	Iryanthera laevis	46**	L
	Macrolobium limbatum	45.1**	L
	Helicostylis scabra	45**	L
	Trichilia laxipaniculata	43.9**	H
	Macrolobium bifolium	43.7**	L
Precipitation of January	*Grias neuberthii*	70**	I
	Macrolobium limbatum	68.7**	H
	Brownea grandiceps	63.2**	I
	Roucheria punctata	50**	H
	Melicoccus novogranatensis	49.3**	I
	Licania heteromorpha	48.8**	H
	Helicostylis scabra	44.7**	H
	Macrolobium bifolium	43.7**	H
	Iryanthera paraensis	43.7**	H
	Perebea guianensis	43.7**	H
Mean diurnal range	*Aniba panurensis*	40.5**	L
	Vitex triflora	36.3**	L
	Anaxagorea brevipes	30.8**	L
	Agonandra silvatica	29.3**	L
	Oxandra euneura	30.8**	L
	Endlicheria metalica	30.8**	L
	Iryanthera tessmannii	30.8**	L

(Table 5.4 continued)

	Swartzia cardiosperma	27.9**	L
	Ocotea acyphylla	29.1**	L
	Simaba orinocensis	23.1*	L
Maximum temperature of the warmest month	*Tetrathylacium macrophyllum*	70.4**	L
	Iriartea deltoidea	70.2**	L
	Chrysochlamys aff. membranacea	66**	L
	Siparuna cf.decipiens	65.4**	L
	Matisia obliquifolia	63.1**	L
	Warszewiczia coccinea	63**	L
	Sterculia frondosa	62.7**	L
	Perebea xanthochyma	61.7**	L
	Maquira calophylla	54.5**	L
	Gustavia longifolia	54.2**	L

B.

Environmental variable	Species	Indicator value	Environmental variable value
Precipitation of the wettest month	*Tetrathylacium macrophyllum*	75.8***	H
	Gustavia longifolia	74.2***	H
	Grias neuberthii	71***	H
	Siparuna cf. *decipiens*	68.5***	H
	Iriartea deltoidea	67***	H
	Naucleopsis glabra	66.1***	I
	Matisia malacocalyx	64.9***	H
	Melicoccus novogranatensis	64.7***	H
	Cordia ucayaliensis	64.7***	I
	Brownea grandiceps	63.3***	H
Precipitation of the driest month	*Melicoccus novogranatensis*	78.6***	H
	Brownea grandiceps	73.1***	H
	Matisia obliquifolia	72.7***	H
	Gustavia longifolia	70.7***	H
	Siparuna cf. *decipiens*	69.9***	H
	Matisia malacocalyx	68***	H
	Protium aidanum	66.3***	H
	Iriartea deltoidea	66.3***	H

(Table 5.4 continued)

	Matisia longiflora	66***	H
	Pentaplaris huaoranica	64.3***	H
Mean diurnal range	*Matisia bracteolosa*	59.7**	L
	Inga auristellae	54.4**	L
	Tetrathylacium macrophyllum	53.3**	H
	Protium subserratum	52.8***	L
	Virola multinervia	51.7**	H
	Grias neuberthii	51.7**	H
	Dendropanax arboreus	48.8**	L
	Aniba panurensis	47.6***	L
	Iryanthera laevis	45.8**	L
	Unonopsis floribunda	44.4**	H
Isothermality	*Siparuna* cf. *decipiens*	72.6***	H
	Protium subserratum	70.3***	L
	Matisia malacocalyx	65.3***	H
	Astrocaryum chambira	63.8***	H
	Iriartea deltoidea	63.4***	H
	Byrsonima putumayensis	62.9***	H
	Sapium marmieri	62.5***	I
	Gustavia longifolia	61.9***	H
	Drypetes amazonica	60.6***	H

A great diversity of genera responded to the environmental variables as important indicators. *Tetrathylacium* and *Grias* were indicators for intermediate precipitation in January and low maximum temperature of the warmest month (Table 5.5). A slightly opposite pattern could be found in *Matayba* and *Osteophloeum*; both were indicators for low precipitation in July and high maximum temperature of the warmest month (Table 5.5). *Tachigali* and *Sacoglottis* were both indicative of low precipitation in July and high precipitation in January. *Iriartea* was the only genus of palms that was identified to indicate low maximum temperature of the warmest month (Table 5.5).

Table 5.5. Results of indicator species analysis (based on genus abundance) for associations with environmental variables. Only top ten genera with the lowest *p* value and then the highest indicator value for each variable are listed. * = $p < 0.1$, ** = $p < 0.05$, *** = $p < 0.01$. H, I, or L represent higher (H), intermediate (I), or lower (L) value of the environmental variable.

Environmental variable	Genus	Indicator value	Environmental variable value
Precipitation of July	*Iryanthera*	67.2**	L
	Casearia	63.9**	I
	Roucheria	48.5**	L
	Sacoglottis	48.2**	L
	Matayba	46.3**	L
	Nealchornea	40.9**	L
	Tachigali	53.7**	L
	Amaioua	40**	L
	Poulsenia	33.9**	H
	Osteophloeum	40.3**	L
Precipitation of January	*Grias*	70.1**	I
	Brownea	64.2**	I
	Hyeronima	59.5**	L
	Swartzia	55.9**	H

(Table 5.5 continued)

	Melicoccus	49.3**	I
	Quararib	48.8**	I
	Roucheria	48.3**	H
	Sacoglottis	48**	H
	Tetrathylacium	47.8**	I
	Tetrameranthus	43.7**	H
Mean diurnal range	*Vochysia*	46.3**	L
	Panopsis	23.1**	L
	Hydrochorea	22.9**	L
	Xylopia	49.2*	L
	Endlicheria	61.9*	L
	Vitex	38.4*	L
	Couratari	37.5*	L
	Dipteryx	26.1*	L
	Borojoa	21.5*	L
	Alseis	30.6*	H
Maximum temperature of the warmest month	*Warszewiczia*	75.9**	L
	Tetrathylacium	74**	L
	Iriartea	70.2**	L
	Perebea	65.4**	L
	Pentagonia	62.8**	L
	Grias	62.4**	L
	Tachigali	62**	H
	Licania	59.3**	H
	Matayba	50.8**	H
	Osteophloeum	47.7**	H

In addition to the continuous environmental variables, I also conducted indicator analysis using categorical variables of vegetation type, geology, and drainage basin (see Chapter 2: Study Area) at both species and genus levels. *Ilex nayana* and *Ilex*, *Cybianthus peruvianus* and *Cybianthus*, as well as *Apeiba membranacea* and *Apeiba*, were indicators of humid lowland hill forests (Table 5.6 and 5.7). For geology,

indicative species/genera for the Neogene Quaternary-Continental period included *Clusia* cf. *columnaris* and *Clusia*, *Grias neuberthii* and *Grias*, *Micandra spruceana* and *Micandra*, and *Mucoa duckei* and *Mucoa* (Table 5.6 and 5.7). For the Amazon basin, both palm species *Astrocaryum murumuru* var. *urostachys* and the genus *Astrocaryum* were indicators.

Table 5.6. Results of indicator species analysis (based on species abundance) for associations with vegetation, geology, and drainage. Only top ten species with the lowest *p* value and then the highest indicator value for each variable are listed. * = $p < 0.1$, ** = $p < 0.05$, *** = $p < 0.01$.

Habitat	Species	Indicator value	Habitat type
Vegetation	*Ilex nayana*	100**	Humid low hill forest
	Neea verticillata	96.7**	Humid low hill forest
	Licania heteromorpha	94**	Humid low hill forest
	Jacaranda macrocarpa	93.7**	Humid low hill forest
	Cybianthus peruvianus	93.1**	Humid low hill forest
	Apeiba membranacea	62.1**	Amazonian lowland evergreen forest
	Sloanea floribunda	83.3**	Humid low hill forest
	Aspidosperma excelsum ssp. *quadrijuga*	82.6**	Humid low hill forest
Geology	*Manilkara inundata*	66.7**	Quaternary Holocene-Continental
	Clusia cf. *columnaris*	100**	Neogene Quaternary-Continental
	Micropholis guyanensis ssp. *duckeana*	100**	Neogene Quaternary-Continental
	Tachigali melinonii	100**	Neogene Quaternary-Continental
	Pouteria oblanceolata	98.2**	Neogene Quaternary-Continental
	Ocotea aciphylla	98.2**	Neogene Quaternary-Continental
	Grias neuberthii	65**	Pliocene-Miocene
	Mucoa duckei	95.5**	Neogene Quaternary-Continental
	Tachigali poeppigiana	91.3**	Neogene Quaternary-Continental
	Micrandra spruceana	89.2**	Neogene Quaternary-Continental

(Table 5.6 continued)

Drainage basin	*Brosimum alicastrum*	98.7**	Amazon
	Hippotis albiflora	97.8**	Amazon
	Cordia mexiana	97.5**	Amazon
	Diospyros subrotata	97.5**	Amazon
	Theobroma obovatum	94.5**	Amazon
	Astrocaryum murumuru var. *urostachys*	86.3**	Amazon
	Virola duckei	84.8**	Amazon
	Siparuna aff. *decipiens*	99**	Tigre
	Chrysophyllum bombycinum	98.9**	Nanay

Table 5.7. Results of indicator species analysis (based on genus abundance) for associations with vegetation, geology, and drainage. Only top ten genera with the lowest p value and then the highest indicator value for each variable are listed. * = $p < 0.1$, ** = $p < 0.05$, *** = $p < 0.01$.

Habitat	Genus	Indicator value	Habitat type
Vegetation	*Ilex*	97.5**	Humid low hill forest
	Micrandra	93.5**	Humid low hill forest
	Ferdinandusa	84.1**	Humid low hill forest
	Cybianthus	89.1**	Humid low hill forest
	Apeiba	52.8**	Amazonian lowland evergreen forest
	Sterigma	66.7**	Humid low hill forest
	Couma	57.3**	Humid low hill forest
	Byrsonima	72**	Humid low hill forest
Geology	*Clusia*	96**	Neogene Quaternary-Continental
	Grias	64.7**	Pliocene-Miocene
	Mucoa	95.5**	Neogene Quaternary-Continental
	Tovomita	89.3**	Neogene Quaternary-Continental
	Caryocar	71.1**	Neogene Quaternary-Continental
	Micrandra	89.2**	Neogene Quaternary-Continental
	Macoubea	83**	Neogene Quaternary-Continental
	Pentagonia	61.2**	Pliocene-Miocene
	Chrysochlamys	55.7**	Pliocene-Miocene
	Roucheria	89.3*	Neogene Quaternary-Continental

(Table 5.7 continued)

Drainage basin	*Hippotis*	98**	Amazon
	Lunania	90.4**	Amazon
	Otoba	85.8**	Amazon
	Astrocaryum	76.7**	Amazon
	Jacaratia	78.5**	Amazon
	Chimarris	99**	Tigre
	Humiria	100**	Nanay
	Ternstroemia	100**	Nanay
	Bauhinia	71.5**	Amazon
	Mucoa	99.6**	Ucamara

Multiple regressions

The extent to which floristic composition at the beta diversity level was associated with a single variable or with combinations of multiple bioclimatic variables was examined using multiple regressions. Multiple regression analyses were conducted with Sørensen's species dissimilarity distance matrices using only the environmental variables that showed the strongest correlations with species/genus ordination axes in NMS and with Sørensen's species dissimilarity in the partial Mantel tests. Overall, all multiple regression models at both species and genus levels were weak. Using only temperature or precipitation variables or combinations of temperature and precipitation did not improve the models' accountability for variance in species or genus abundance (Table 5.8). The percentage variance in species and genus abundance accounted for by combinations of temperature and precipitation variables in descending orders of importance ranged between 15%-31% and 9%-18%, respectively (Table 5.8A). When the subset of 37 plots was used in the analysis, the percentage variance in species abundance accounted for by combinations of temperature and precipitation variables ranged between 17%-42% (Table 5.8B). More specifically, the combinations that

included one or two precipitation variables accounted for > 25% of percentage variance in species abundance (Table 5.8B).

Table 5.8. Multiple regression models using only the environmental factors that showed significant correlations with the floristic composition in NMS ordinations and the partial Mantel tests using plot data of 49 plots (A) and 37 subset plots (B). * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.0001$.

A.

Level	Variables	Regression on matrices model	R^2
Species abundance	Mean diurnal range (1)	0.8** + 0.03 (1**)	0.15**
Genus abundance		0.63** + 0.03 (1**)	0.09**
Species abundance	Max. temperature of	0.78** + 0.01 (2**)	0.21**
Genus abundance	the warmest month (2)	0.6** + 0.01 (2**)	0.14**
Species abundance	Precipitation in January (3)	0.78** + 0.002 (3**)	0.17**
Genus abundance		0.62** + 0.001 (3**)	0.09**
Species abundance	Precipitation in July (4)	0.8** + 0.001 (4**)	0.17**
Genus abundance		0.63** + 0.001 (4**)	0.09**
Species abundance	(1) + (2)	0.76** + 0.02 (1**) + 0.008 (2**)	0.27**
Genus abundance		0.59** + 0.02 (1**) + 0.008 (2**)	0.17**
Species abundance	(3) + (4)	0.76** + 0.001 (3**) + 0.007 (4**)	0.24**
Genus abundance		0.6** + 0.001 (3**) + 0.001 (4**)	0.13**

(Table 5.8 continued)

Species abundance	(1) + (3)	0.78** + 0.01 (1**) + 0.001 (3**)	0.2**
Genus abundance		0.61** + 0.01 (1**) + 0.001 (3**)	0.11**
Species abundance	(1) + (4)	0.77** + 0.02 (1**) + 0.001 (4**)	0.26**
Genus abundance		0.6** + 0.02 (1**) + 0.001 (4**)	0.14**
Species abundance	(2) + (3)	0.74 ** + 0.008 (2**) + 0.001 (3**)	0.3**
Genus abundance		0.57 ** + 0.008 (2**) + 0.001 (3**)	0.18**
Species abundance	(2) + (4)	0.77** + 0.007 (2**) + 0.0004 (4**)	0.23**
Genus abundance		0.6** + 0.009 (2**) + 0.0002 (4**)	0.14**
Species abundance	(1) + (2) + (3) + (4)	0.75** + 0.01 (1**) + 0.006 (2**) + 0.0007 (3**) + 0.0002 (4**)	0.31**
Genus abundance		0.58** + 0.007 (1**) + 0.008 (2**) + 0.0007 (3**) + 0.0006 (4**)	0.18**

B.

Level	Variables	Regression on matrices model	R^2
Species abundance	Mean diurnal range (1)	0.75** + 0.03 (1**)	0.22**
Species abundance	Isothermality (2)	0.75** + 0.003 (2**)	0.13**
Species abundance	Precipitation of the wettest month (3)	0.75** + 0.003 (3**)	0.25**

(Table 5.8 continued)

Species abundance	Precipitation of the driest month (4)	0.73** + 0.003 (4**)	0.25**
Species abundance	(1) + (2)	0.75** + 0.03 (1**) + 0.007 (2*)	0.23**
Species abundance	(3) + (4)	0.7** + 0.002 (3**) + 0.002 (4**)	0.39**
Species abundance	(1) + (3)	0.72** + 0.02 (1**) + 0.002 (3**)	0.23**
Species abundance	(1) + (4)	0.72** + 0.02 (1**) + 0.002 (4**)	0.32**
Species abundance	(2) + (3)	0.72 ** + 0.02 (2**) + 0.002 (3**)	0.31**
Species abundance	(2) + (4)	0.72** + 0.009 (2**) + 0.003 (4**)	0.26**
Species abundance	(1) + (2) + (3) + (4)	0.69** + 0.02 (1**) - 0.007 (2**) + 0.002 (3**) + 0.002 (4**)	0.42**

DISCUSSIONS

This beta diversity study excluded all morphospecies that occurred in each plot in order to avoid unreliable species-level comparisons. As a result, multiple morphospecies were removed from the datasets in southeastern and northeastern Ecuador. The removal eliminated uncertainty in species composition, but might cause potential bias in species diversity. The only solution to such bias would be to compare vouchers of morphospecies from all 49 plots or the 37 subset plots and reassign morphospecies identifications. Unfortunately the vouchers have been stored in multiple herbaria in Ecuador and Peru and are not easily accessed due to the logistics.

The results in Table 5.1 are complementary to some previous comparative studies between tree flora in Yasuní National Park, Ecuador and in Manu National Park in Madre de Dios, southeastern Peru (Pitman et al. 2001, 2002), as well as Loreto (northern Peru) and Madre de Dios (Phillips et al. 2003b). This dissertation showed that both average stem density/ha and species richness/ha were lower in plots in northeastern Ecuador (including Yasuní) than in Loreto (Peru). Pitman et al. (2001, 2002) concluded that forests in Yasuní are more diverse at all spatial scales and all taxonomic levels than in Manu. Phillips et al. (2003b) found that species richness and Fisher's alpha diversity in the aseasonal, equatorial forests in Loreto are much higher than in the seasonal forests in Madre de Dios. Hence, I argue that the very species-rich Loreto may have the most diverse tree flora in the western Amazon, followed by eastern Ecuador and then by southeastern Peru. This finding is consistent with the argument made by Bass et al. (2010) that eastern Ecuador and northern Peru are species richness centers for multiple taxa and are among the most biodiverse places on Earth.

Species commonness and rarity are indicative characteristics of heterogeneity in beta species diversity patterns at the regional scale. Pitman et al. (2001) defined a threshold density of common species at the landscape scale as ≥ 1 individual/ha among the plots in each geographic region in Ecuador and Peru. According to this threshold, species represented by at least 3, 34, and 12 individuals/ha in southeastern Ecuador, northeastern Ecuador, and Loreto, respectively, qualified as common at the landscape scale while species with only one stem per hectare in each region were considered very rare. When the subset of 37 plots was used for the analysis, common species were defined as species with at least 3, 23, and 11 individuals/ha in southeastern Ecuador, northeastern Ecuador, and Loreto, respectively. Different from plots in the networks of northeastern Ecuador and Peru, the three 1-ha plots that I established in southeastern Ecuador harbored both common and extremely rare species, as well as species that were shared by plots in Ecuador and Peru. There were similar or lower percentages of common species in northeastern Ecuador and Loreto than in Yasuní and Manu, respectively (Table 5.9). Northeastern Ecuador harbored fewer extremely rare species than Yasuní, but Loreto had a higher percentage of very rare species than Manu (Table 5.9). The high percentages of both common and extremely rare species in southeastern Ecuador suggested the coexistence of potential habitat specialists and generalists at the landscape scale. It is possible that the plots in southeastern Ecuador are located in a transitioning region of tree biogeography in western Amazon, and therefore have a higher percentage of shared species.

The plot distribution in ordination space at both species (Figure 5.3) and genus (Figure 5.4) levels corresponded to this argument, as plots in southeastern Ecuador were located in a central ordination space between plots in regions of northeastern Ecuador and northern Peru. Distribution of the 37 subset plots in ordination space (Figure 5.3B)

indicated greater distinction between western (Ecuadorian) and eastern (Peruvian) plots, as well as geographic correspondence of plot locations. In contrast, both plots in Loreto and Yasuní had much higher percentages of extremely rare species than common species, indicating greater occurrence of habitat specialists that might contribute to the very species rich tree communities in those regions.

Table 5.9. Percentages of common and rare species in different regions of inventory plots. The table also shows percentages of shared and shared common species among three study regions in this dissertation (A = all 49 plots, B = 37 subset plots), and between two regions studied by Pitman et al. (2001).

A.

	Common species	Rare species	Shared species	Shared common species	Reference
Southeastern Ecuador	34.9	46.1	50.1	6.1	
Northeastern Ecuador	11.5	17.1	15.4	1.9	
Loreto, Peru	14.4	34.7	17.6	2.1	
Yasuní, Ecuador	15	26.9	26	14.7	Pitman et al. 2001
Manu, Peru	22	25.4	36.7	21.6	Pitman et al. 2001

B.

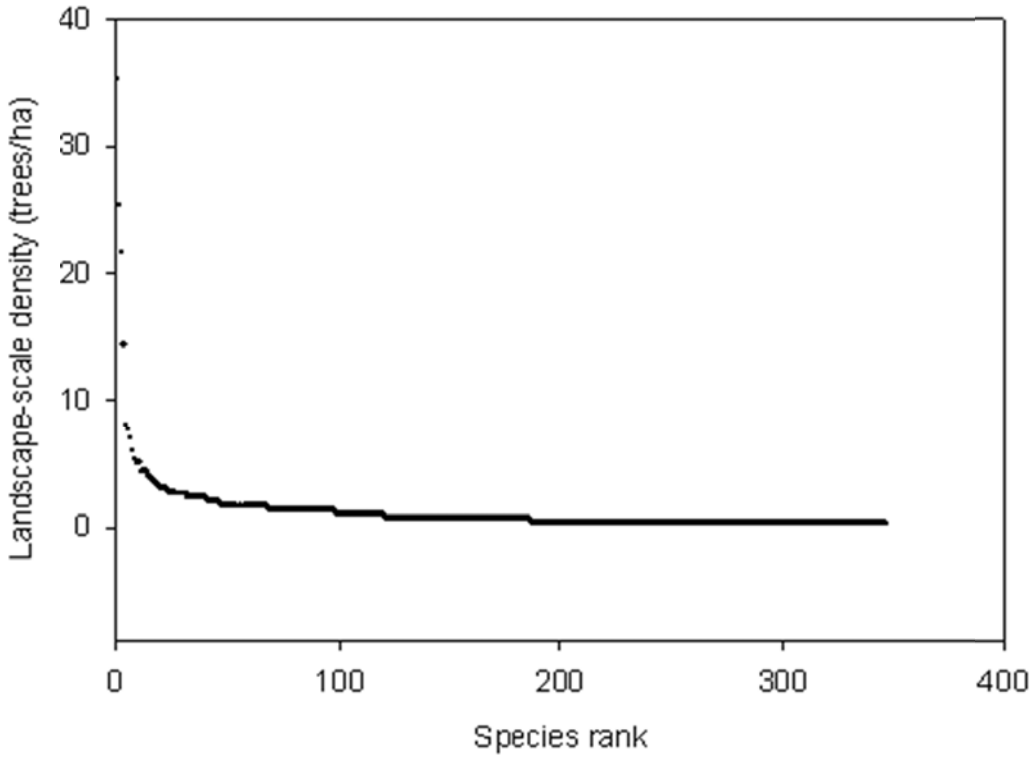
	Common species	Rare species	Shared species	Shared common species
Southeastern Ecuador	34.9	46.1	48.4	4.9
Northeastern Ecuador	14.2	20.9	16.2	1.6
Loreto, Peru	14.6	35.8	17.6	1.8

Although most species showed landscape-level densities of < 1 individual/ha (Table 5.9), a great number of trees in the Ecuadorian and Peruvian forests belonged to a small set of common species of high local abundance. For instance, the common species in southeastern and northeastern Ecuador as well as Loreto respectively accounted for 77.6%, 60.6% (63.8% using the subset data), and 61% of total tree abundance. These common species combine high frequency with high local abundance, forming "oligarchies" as defined by Pitman et al. (2001). The dominance patterns were consistent with the "oligarchies" comprised by common species in Yasuní and Manu, in which oligarchic species occupied 63% and 73% of all stems, respectively (Pitman et al. 2001). A study that tested this oligarchy hypothesis in Yasuní and Maldidi (Bolivia) found strong evidence that western Amazonian forests can be dominated by oligarchies of species, genera, and families (Marcia and Svenning 2005). Table 5.2 indicated that the top three oligarchic species in the three 1-ha plots in southeastern Ecuador all had landscape scale density > 20 trees/ha, whereas in Loreto none of the oligarchic species had landscape scale density > 12 trees/ha. The oligarchy in northeastern Ecuador displayed a pattern similar to Loreto, with an exception of an outlier oligarchic member of very high landscape-scale density, *Iriartea deltoidea* (a canopy palm species) (Figure 5.6B). *Iriartea deltoidea* is also the most common and abundant species in Yasuní and Manu, performing as a statistical outlier (Pitman et al. 2001). In particular, the oligarchy in southeastern Ecuador mainly came from a small number of species with high landscape-scale density, whereas in Loreto the oligarchy was formed by a larger number of species with relatively lower density (Figure 5.6A, C). Therefore, species oligarchy appeared to be more prominent in southeastern Ecuador than in northeastern Ecuador and northern Peru. The pronounced oligarchy in southeastern Ecuador may explain why the diversity indices are lower compared to plots in northeastern Ecuador and Peru.

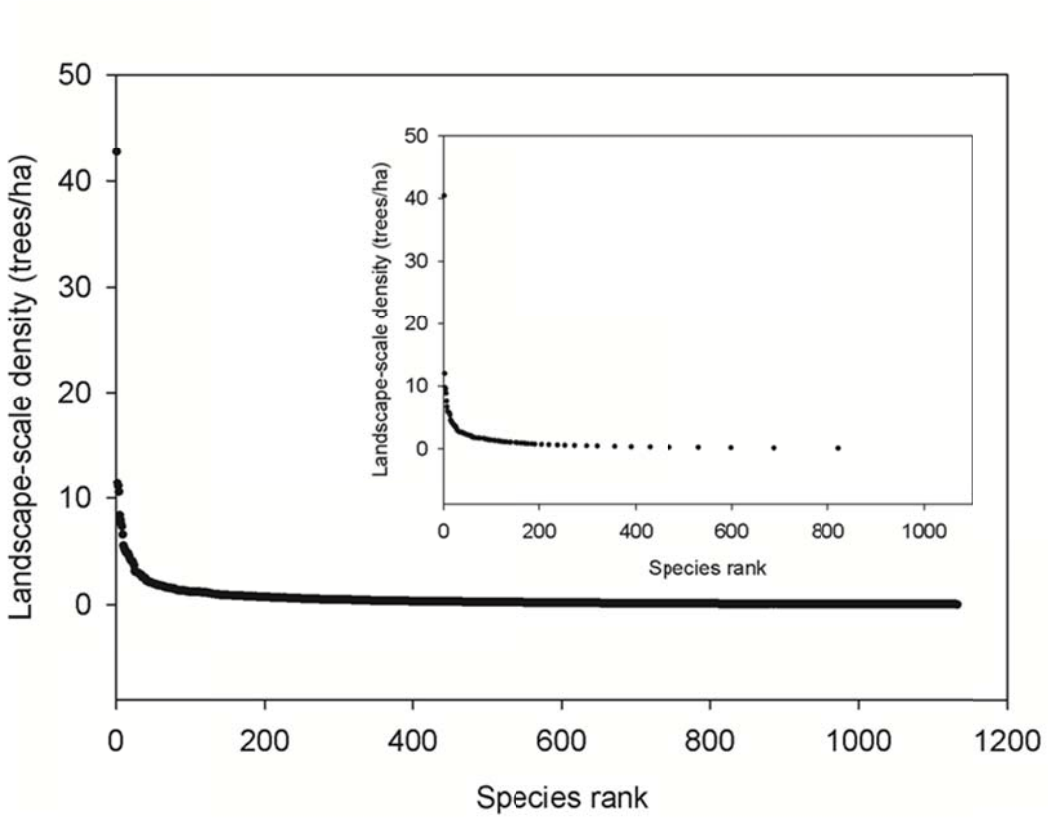
Oligarchy in the Amazonian tree communities in different regions of Ecuador and Peru suggests non-random occurrences of common species, which play an important role of influencing relative tree abundance. In the following sections I discuss patterns of oligarchy and potential mechanisms that could cause these patterns.

Figure 5.6. Distribution of tree density at the landscape scale in southeastern (A) and northeastern (B) Ecuador, and Loreto in Peru (C). The smaller figures in 5.6B and 5.6C represent distributions using the subset plots.

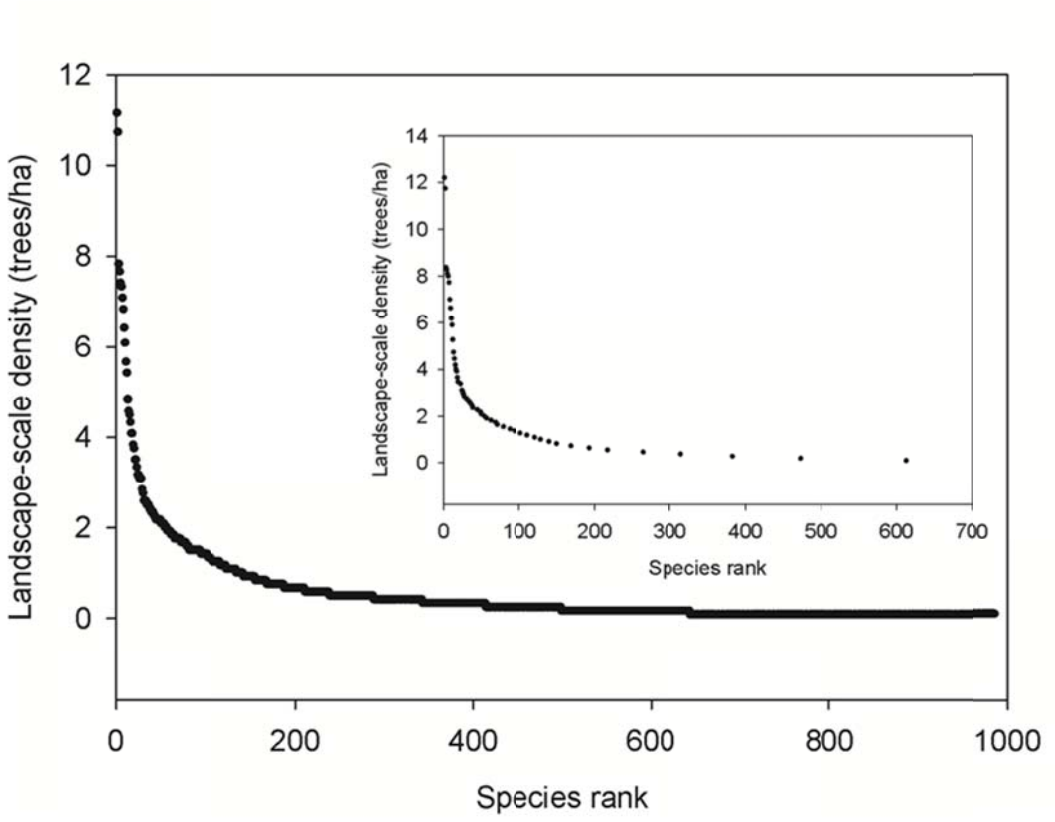
A.



B.


Landscape-scale density (trees/ha)
Species rank
0
200
400
600
800
1000
1200
10
20
30
40
50
Landscape-scale density (trees/ha)
Species rank
0
200
400
600
800
1000
10
20
30
40
50

C.



Plots in northeastern Ecuador, southeastern Ecuador, and Loreto (Peru) shared 174 species, which accounted for 50% of total number of species in southeastern Ecuador (Table 5.9A). The number of shared species decreased to 168 when the subset of 37 plots was analyzed and these species still accounted for 48.4% of total number of species in southeastern Ecuador (Table 5.9B). In contrast, these shared species only accounted for less than 18% of total number of species in northeastern Ecuador or Loreto, Peru. The decrease in percentage within total number of species for common species (i.e. $\geq$ 1 individual/ha) that were shared by all three regions indicated that many common species may have limited distribution ranges (Table 5.9). The shift in species composition and discontinuity in a larger portion of tree species between the western and eastern plots of

the study region were consistent with the observation by Pitman et al. (2008). The sharp decrease in percentage of shared species from the direction of southeastern to northeastern Ecuador and northern Peru could rise from two possibilities. First, there may be a missing link of tree biogeography characterization in central-eastern Ecuador which would provide evidence of a more gradual gradient in decreased percentage of shared species. Second, the three 1-ha plots in southeastern Ecuador may be in a unique, isolated regional patch to which a great number of species disperse and overlap. These species were able to establish in southeastern Ecuador perhaps because of certain favorable edaphic, topographic, or hydrological conditions there (e.g. no distinct dry season). A more detailed study in the future should focus on comparing the bioclimatic and biophysical environment where these species were found across the three regions and elsewhere in the world.

Several common species showed a gradient of decrease in stem density from the western to the eastern plots. The density of *Iriartea deltoidea* declined from over 40 stems/ha in northeastern Ecuador, 22 in southeastern Ecuador, to just above 1.4 in Loreto. Likewise, *Matisia malacocalyx* also had a reduced stem density from above 8.4 stems/ha in northeastern Ecuador to above 1.4 individual/ha in Loreto. Another palm species *Oenocarpus batatua* showed decrease in stem density from 25 stems/ha in southeastern Ecuador to just above 7 stems/ha in northeastern Ecuador and Loreto. The discontinuity also occurred from the eastern to the western plots when for instance, the dominant palm *Astrocaryum murumuru* decreased from over 11 stems/ha to less than 5 stems/ha in northeastern Ecuador and zero in southeastern Ecuador. This dissertation study supported the observation made by Pitman et al. (2001) of oligarchic tree species in the Amazon and discontinuity of some oligarchic species between the eastern and the western parts of the study region (Pitman et al. 2008). Like what Pitman et al. (2001) predicted, such

oligarchy did not occur at random. Estimates of the probability of finding the same shared species among the most common species (using the method by Pitman et al. 2001) in southeastern Ecuador vs. northeastern Ecuador, northeastern Ecuador vs. Peru, and southeastern Ecuador vs. Loreto under non-equilibrium community drifts were $< 10^{-5}$.

Oligarchy and discontinued oligarchy have also been documented by other Amazonian studies. For example, palms that are abundant in Yasuní, Ecuador are not abundant in Iquitos, Peru. Most Ecuadorian palm distribution ranges reach Iquitos but not the reverse (Montufar et al. 2006). The floristic composition of oligarchy in Yasuní and Iquitos are more strongly related to geographic distances than environmental variables. Some dominant palms in Iquitos but not in Yasuní are limited by dispersal and variation in environmental conditions across scales (Vormisto et al. 2004). Kristiansen et al. (2009) also found scale-dependency of commonness in Amazonian palms, which is related to local abundance and continental dispersal distribution. Although oligarchy is pronounced at all levels, dominance and consistency of relative abundance ranks are the strongest at family level according to Marcia et al. (2005). Recently Pitman et al. (personal communication) discovered some changes in the oligarchy and discontinued oligarchy patterns in western Amazon after establishing new inventory plots near the Putumayo River. The unpublished findings by Pitman et al. implied that as biogeographers continue to gain knowledge of tree diversity, distribution, and dominance, our understanding of beta diversity may improve.

The discontinuity in species composition and decrease in oligarchy may be the major contributors to the high beta diversity in western Amazon, as well as the main drivers of species rarity that necessitates conservation attention in the Amazon. Sørensen's dissimilarity index between paired plots showed a minimum of 44% and a maximum of 100% difference in species composition. In a couple of recent studies that

examined beta diversity among over 50 plots from the Andean foothills to Brazil, species dissimilarity is found slightly less pronounced than what I discovered in this dissertation research (Pitman et al. 2008, Coronado et al. 2009). By using ordination techniques to examine potential species assemblages at the beta diversity level, I found that floristic variation between the Amazonian plots in NMS ordination space formed two visually discernible clusters, independent of the geographic locations of those plots (Figure 5.3). Southeastern Ecuador, northeastern Ecuador, and Loreto, Peru all appeared to harbor very unique groups of species that represent distinct geographic regions. These unique species groups, as observed by Gentry (1988) that the "predictability" of floristic composition and tropical tree diversity are represented by environmental parameters, were more affected by precipitation than by edaphic factors. In the following discussion I aim to examine the extent to which environmental variables affect floristic variation in these regions as part of the path towards understanding potential drivers of beta diversity patterns.

Kendall's Tau correlations indicated intermediate associations between the ordination axes and precipitations in January, February, June, and July, as well as mean temperature of the wettest quarter for an inference of how climate might affect the floristic variation in the Amazon. Further examinations using the partial Mantel tests proved that climatic variables, rather than topography, were correlated to species diversity (at least 61 out of 67 climatic and bioclimatic variables showed significant results). What dictated the climatic variability might be the seasonal variation particularly in precipitation. Temperature among the plots show homogeneity in annual mean temperature (24.7-26.8°C), mean diurnal range (9.3-10.1°), and annual range (11.1-12.2°). In contrast, the quantity and distribution of precipitation indicate great heterogeneity and a broad range of precipitation seasonality among the plots.

The above finding shows congruence with other broad-scale Amazonian studies. Stropp et al. (2009) concluded that regional diversity is correlated with paleo-climatic stability and rainfall seasonality. Ter Steege et al. (2006) discovered two dominant gradients in tree composition and function in the Amazon, one paralleling with soil fertility and the other paralleling with dry season length. The first gradient suggested that the western Amazon has more recently deposited sediments which induce higher soil fertility and species turnover rate. The second gradient showed how dry season length limits tree diversity in the Amazon and its important influence on the geographic variation in tree community composition (ter Steege et al. 2006). This dissertation research also revealed a relationship between beta diversity and climatic factors, but direct examinations of how seasonality plays a role in governing beta diversity are still required. In particular, future research should examine whether or not rainfall seasonality regulates tree diversity patterns by affecting species shade tolerance and functional type, as suggested by ter Steege et al. (2003).

Among the species-rich tree communities in western Amazon, a few palm species were found to be indicator species for particular climatic variables. Palms were also among the species that showed the most pronounced shift in oligarchy between the Ecuadorian and Peruvian plots. I argue that palms are among the most useful taxa for beta diversity studies in the Amazon. First, the distinctive umbrella-like crowns make palms the most discernible species in rapid ground inventories. Second, multiple studies have shown how palm diversity and distributions are associated with various environmental attributes (e.g. Svenning 2001a, 2001b, Vormisto et al. 2004, Kristiansen et al. 2009). Third, palms provide great opportunities in examining dominance and rarity at local and landscape scales (e.g. Pitman et al. 2001). Finally, the high discernibility of palm canopies allows a potential of studying palm diversity and distribution using remote

sensing data. As an exploratory study if how palms could function as the target taxonomic group for biodiversity research using remotely sensed data, in the next chapter I study the spatial distributions of three canopy palm species using aerial photographs.

Numerous studies have aimed to elucidate which environmental factors and to what extent beta diversity of tropical trees is impacted by the biophysical environment. Floristic responses to variation in soil characteristics have been found in Iquitos in northern Peru (Vormisto et al. 2004, Ruokolainen et al. 2007), whereas associations with topography, or topography linked with climate and/or geology were discovered in montane/premontane Peru and in the Ecuadorian Amazon (La Torre-Cuadros et al. 2007, Queenborough et al. 2007). In India, beta diversity is highest in regions of the strongest rainfall gradients and seasonality (Davidar et al. 2007). However, more studies have revealed the complex and synergistic effects of multiple factors. For instance, in Bolivia beta diversity has greater correlations with edaphic factors for large trees but for smaller trees geographic distance between sites plays a more important role (Marcia et al. 2007). In another study in Bolivia, the floristic variation is found strongly associated with differences in water availability and temperature, suggesting that climatic gradient shapes tree diversity more than edaphic factors (Toledo et al. 2010). Both edaphic and topographic characteristics affect the floristic patterns in Ecuador and Peru (Thessler et al. 2005, Poulen et al. 2006). Both environmental variation (especially soil) and geographic distance are important, but substrate-mediated local processes play a greater role in influencing beta diversity patterns in Peru than distance-dependent processes (Phillips et al. 2003a). In this dissertation study how variation in edaphic factors (e.g. soil moisture, soil characteristics, or soil chemistry) contributed to the floristic variation was not examined due to the difficulty in obtaining soil data. It is possible that a gradient of soil characteristics exists and may influence beta diversity patterns in western Amazon.

Future research should dedicate efforts in obtaining edaphic information of the plots in which soil data were collected and examine whether or not heterogeneity of soils is associated with beta diversity. Similar to the alpha diversity study in Chapter 4 regarding the limitation in data availability, this study of beta diversity does not exclude potential biological niche partitioning resulting from interspecific competition.

Hence, do the abovementioned studies and this dissertation research shed any light on what governs beta diversity of trees in the Amazon? The pervasive associations between beta diversity, soil factors, and geographic distance suggest that niche partitioning determines species diversity in Borneo (Paoli et al. 2006). Topographic niche partitioning is found in Yasuní National Park in Ecuador, although species similarity also declines with increasing geographic distance (Valencia et al. 2004a). Another well-discussed mechanism is dispersal limitation. The patchiness of diversity patterns observed in Yasuní is said to mostly be related to dispersal limitation (Valencia et al. 2004b). Species distribution in Panama is determined by dispersal limitation more than by environmental heterogeneity. Spatial variation is more important than combined impact of environmental factors and geographic distance (Chust et al. 2006). Hubbell (2010) argued that species evolve to be generalists when the landscape is patchy and the species is a poor disperser, and vice versa.

Tuomisto et al. (2003c) concluded that the unified neutral theory (Hubbell 2001) over large areas in the Amazon is not supported. Instead, random but spatially autocorrelated species composition resulting from dispersal limitation and patchy but environmentally determined diversity patterns are discovered (Tuomisto et al. 2003c). Ter Steege (2010b) also claimed that no tree community characteristics (e.g. abundance of common species and species similarities) in the Guyana Shield are consistent with neutral theory. McGill and Nekola (2010) found that neutrality does not appear to be

important while dispersal limitation and regional replacement appear to be more critical in imposing diversity.

This dissertation study observed species oligarchy and shifts in oligarchy, which implied dispersal limitation of at least dominant species. Dispersal limitation or regional differentiation/replacement is again implied based on the significant relationship between variation in floristic composition and geographic distances between paired plots. Among all the bioclimatic factors, variables associated with rainfall seasonality showed significant relationships with species composition. Based on the results of this dissertation chapter, I propose that dispersal limitation and climate, especially precipitation seasonality, may be potentially the most important factors that contribute to tree beta diversity in western Amazon.

Chapter 6: Remote sensing-based patterns of canopy shadows and palms in southeastern Ecuador

RESULTS

Canopy shadows from aerial photographs

Accuracy assessment of canopy shadow extractions

Spatial distribution and patch patterns of canopy shadows are part of characteristics of forest canopy properties that are informative for understanding alpha diversity at the local, fine scale. In this chapter I present the distribution of canopy shadows based on object-based classification results using fine-resolution aerial photographs. I then show dominant palm identification using aerial photographs. Overall, in both Yutsuntsa and Sawastian communities, the pixel-based sampling for accuracy assessment showed higher producer's and user's accuracies in classifying both canopy shadow and non-shadow classes than the object-based sampling. Mean producer's and user's accuracies for the two classes in Yutsuntsa were 90%-92% when using pixel-based sampling and were 86%-89% according to object-based sampling. With accuracies slightly lower in Sawastian, the pixel-based sampling showed 86%-92% mean producer's and user's accuracies for the two classes, whereas the object-based sampling showed 84%-89% accuracies (Table 6.1). Likewise, mean overall accuracies of the pixel- vs. object-based sampling methods were 91% and 88% in Yutsuntsa and 89% and 86% in Sawastian, respectively (Table 6.1).

In Yutsuntsa, the average conditional Kappa for both canopy shadow and non-shadow classes using pixel-based sampling were over 0.8, reaching an "almost perfect" agreement between classified and reference data according to the interpretation of Kappa statistics provided by Ladis and Koch (1977). The average conditional Kappa for both canopy shadow and non-shadow classes using object-based sampling were under 0.8, but

were still considered to have a "substantial" agreement between classified and reference data (Table 6.1). A higher average overall Kappa was shown in pixel-based sampling than in object-based sampling. Z statistics for both sampling methods exceeded a threshold value of 1.96 at a 95% confidence interval, indicating that the classifications were much better than random placement of pixels (Table 6.1). The average conditional and overall Kappa values according to pixel-based sampling were higher than object-based sampling in Sawastian. All Kappa values suggested at least a substantial agreement between classified and reference data according to Landis and Koch (1977), especially for the conditional Kappa of non-shadow class using pixel-based sampling, which reached an "almost perfect" agreement (Table 6.1). Similar to the observation in Yutsuntsa, the Z statistics in Sawastian indicated that the classifications were much better than random placement of pixels (Table 6.1).

Table 6.1. Summary of mean ± SE of producer's accuracy, user's accuracy, overall accuracy, conditional Kappa, overall Kappa, and Z statistics for error matrices constructed in pixel-based and object-based sampling methods in Yutsuntsa and Sawastian.

Method	Mean ± SE of the measures					
	Producer's accuracy (%)	User's accuracy (%)	Overall accuracy (%)	Conditional Kappa	Overall Kappa	Z statistics
Yutsuntsa						
Pixel-based			91.1±1.11		0.82±0.02	21.59±1.69
Shadow	92.1±1.2	90±1.42		0.81±0.03		
Non-shadow	90.3±1.33	92.21±1.26		0.84±0.02		
Object-based			87.62±1.44		0.75±0.03	17.63±2.12
Shadow	88.85±1.48	86.15±2.16		0.74±0.04		
Non-shadow	86.79±1.87	89.08±1.56		0.78±0.03		
Sawastian						
Pixel-based			89.34±0.6		0.79±0.01	19.05±1.17
Shadow	91.43±0.85	86.9±0.98		0.75±0.02		
Non-shadow	87.57±0.83	91.78±0.87		0.84±0.02		
Object-based			86.7±0.97		0.74±0.02	16.52±1.07
Shadow	89.1±1.23	84.45±1.42		0.71±0.02		
Non-shadow	85.31±1.19	89.55±1.3		0.79±0.03		

The pixel-based sampling showed higher producer's, user's, and overall accuracies than the object-based sampling in almost all images in Yutsuntsa and Sawastian. For the canopy shadow class, producer's and user's accuracies in Yutsuntsa were 1.5%-9% and 1%-12%, respectively, higher in pixel-based sampling than in object-based sampling whereas in Sawastian the respective differences were 1.4%-7% and 0%-8% (Table 6.2A, B). For the non-shadow class, pixel-based sampling in Yutsuntsa had 1.6%-12% and 0.9%-9%, respectively, greater producer's and user's accuracies than object-based samplings (Table 6.2A). In Sawastian, 0%-7% and 1.3%-7.5% respective differences in producer's and user's accuracies between pixel-based vs. object-based samplings were found (Table 6.2B). Similarly, pixel-based sampling showed greater overall accuracy than object-based sampling for both Yutsuntsa and Sawastian. Differences in overall accuracy between the two sampling methods were 2%-10% in Yutsuntsa and 0.8%-7% in Sawastian (Table 6.2A, B). Both methods for assessing classification accuracies performed well, but the object-based sampling approach appeared to be more congruent with the classification unit, which was based on individual "objects" of canopy shadows.

The conditional Kappa for canopy shadow and non-shadow classes in both Yutsuntsa and Sawastian had greater values according to pixel-based sampling method than object-based sampling. Pixel-based sampling also showed higher overall Kappa in both Yutsuntsa and Sawastian than object-based sampling (Table 6.2A, B). All conditional and overall Kappa values in pixel-based and object-based samplings reached "almost perfect" or "substantial" agreement between classified and reference data according to the interpretation by Landis and Koch (1977). Z statistics indicated that all classifications in Yutsuntsa and Sawastian were much better than random pixel placement ($Z > 1.96$ at a 95% confidence interval) (Table 6.2A, B). In Yutsuntsa, the

pairwise Z statistics in five out of nine images showed significant differences between error matrices using pixel-based vs. object-based samplings ($Z > 1.96$). For Sawastian, significant differences between error matrices using pixel-based vs. object-based samplings occurred in two out of nine images ($Z > 1.96$) (Table 6.2A, B).

Table 6.2. Individual producer's accuracy, user's accuracy, overall accuracy, conditional Kappa, overall Kappa, Z statistics, and pairwise Z statistics for error matrices constructed using pixel-based and object-based sampling methods in each image in Yutsuntsa (A) and Sawastian (B). * = significant difference in pairwise Z statistics.

A.

Method	Sample size	Producer's accuracy (%)	User's accuracy (%)	Overall accuracy (%)	Conditional Kappa	Overall Kappa	Z statistics	Pairwise Z
Mosaic C								3.56*
Pixel-based				94.76		0.9	29.11	
Shadow	105	93.52	96.19		0.92			
Non-shadow	105	96.08	93.33		0.87			
Object-based				84.29		0.69	13.65	
Shadow	105	84.62	83.81		0.68			
Non-shadow	105	83.96	84.76		0.69			
Mosaic B								2.55*
Pixel-based				92.27		0.85	23.48	
Shadow	110	94.29	90		0.81			
Non-shadow	110	90.43	94.55		0.89			
Object-based				84.55		0.69	14.18	
Shadow	110	89.58	78.18		0.61			
Non-shadow	110	80.65	90.91		0.79			
Mosaic D								2.34*
Pixel-based				89.11		0.78	19.78	
Shadow	124	92.92	84.68		0.72			

(Table 6.2 continued)

Non-shadow	124	85.93	93.55		0.86		
Object-based				94.8		0.9	31.9
Shadow	124	94.44	95.2		0.9		
Non-shadow	124	95.16	94.4		0.89		
Mosaic A							2*
Pixel-based				91.1		0.82	22.18
Shadow	118	94.5	87.29		0.76		
Non-shadow	118	88.19	94.92		0.89		
Object-based				85.17		0.7	15.2
Shadow	118	91.09	77.97		0.61		
Non-shadow	118	80.74	92.37		0.82		
Mosaic E							1.97*
Pixel-based				95.14		0.9	25.19
Shadow	72	94.52	95.83		0.92		
Non-shadow	72	95.77	94.44		0.89		
Object-based				88.89		0.78	14.85
Shadow	72	90	87.5		0.76		
Non-shadow	72	87.84	90.28		0.8		
Mosaic F							1.51
Pixel-based				93.18		0.86	25.41
Shadow	110	92.79	93.64		0.87		
Non-shadow	110	93.58	92.73		0.86		
Object-based				89.09		0.78	18.6
Shadow	110	87.07	91.82		0.83		

(Table 6.2 continued)

Non-shadow	110	91.35	86.36		0.74			
Mosaic H								1.31
Pixel-based				87.62		0.75	16.24	
Shadow	101	88	87.13		0.75			
Non-shadow	101	87.25	88.12		0.76			
Object-based				91.58		0.83	21.29	
Shadow	101	94.68	88.12		0.78			
Non-shadow	101	88.89	95.05		0.89			
Mosaic I								0.9
Pixel-based				85		0.7	12.4	
Shadow	80	84.15	86.25		0.72			
Non-shadow	80	85.9	83.75		0.68			
Object-based				80.63		0.61	9.8	
Shadow	80	81	80		0.61			
Non-shadow	80	80.25	81.25		0.62			
Mosaic G								0.76
Pixel-based				91.76		0.84	20.49	
Shadow	91	94.19	89.01		0.79			
Non-shadow	91	89.58	94.51		0.88			
Object-based				89.55		0.79	19.17	
Shadow	91	87.18	92.73		0.84			
Non-shadow	91	92.23	86.36		0.74			

(Table 6.2 continued)

B.

Method	Sample size	Producer's accuracy (%)	User's accuracy (%)	Overall accuracy (%)	Conditional Kappa	Overall Kappa	Z statistics	Pairwise Z
Mosaic B								2.05*
Pixel-based				88.62		0.77	19.07	
Shadow	123	89.92	86.99		0.75			
Non-shadow	123	87.4	90.24		0.8			
Object-based				82.11		0.64	13.14	
Shadow	123	84.35	78.86		0.61			
Non-shadow	123	80.15	85.37		0.69			
Mosaic A								1.97*
Pixel-based				89.93		0.8	22.91	
Shadow	149	91.03	88.59		0.78			
Non-shadow	149	88.89	91.28		0.82			
Object-based				84.56		0.69	16.51	
Shadow	149	84.11	85.23		0.7			
Non-shadow	149	85.03	83.89		0.68			
Mosaic C								1.47
Pixel-based				91.67		0.83	23.9	
Shadow	126	90.7	92.86		0.85			
Non-shadow	126	92.68	90.48		0.81			
Object-based				87.7		0.75	18.22	
Shadow	126	86.26	89.68		0.79			

(Table 6.2 continued)

Non-shadow	126	89.26	85.71		0.73		
Mosaic F							1.18
Pixel-based				90.27		0.81	20.42
Shadow	113	91.74	88.5		0.78		
Non-shadow	113	88.89	92.04		0.83		
Object-based				86.73		0.73	16.27
Shadow	113	89.52	83.19		0.69		
Non-shadow	113	84.3	90.27		0.79		
Mosaic D							0.54
Pixel-based				89.04		0.78	15.1
Shadow	73	93.85	83.56		0.7		
Non-shadow	73	85.19	94.52		0.88		
Object-based				86.99		0.74	13.28
Shadow	73	90.91	82.19		0.68		
Non-shadow	73	83.75	91.78		0.82		
Mosaic E							0.43
Pixel-based				86.45		0.73	15.58
Shadow	107	87.5	85.05		0.71		
Non-shadow	107	85.45	87.85		0.75		
Object-based				87.85		0.76	16.95
Shadow	107	94.51	80.37		0.66		
Non-shadow	107	82.93	95.33		0.89		

(Table 6.2 continued)								
Mosaic H								0.38
Pixel-based				91.67		0.83	20.89	
Shadow	96	96.51	86.46		0.75			
Non-shadow	96	87.74	96.88		0.93			
Object-based				92.71		0.85	22.76	
Shadow	96	93.62	91.67		0.84			
Non-shadow	96	91.84	93.75		0.87			
Mosaic G								0.33
Pixel-based				87.18		0.74	13.89	
Shadow	78	90.28	83.33		0.69			
Non-shadow	78	84.52	91.03		0.81			
Object-based				85.9		0.72	12.88	
Shadow	78	88.89	82.05		0.67			
Non-shadow	78	83.33	89.74		0.78			
Mosaic I								0.29
Pixel-based				89.26		0.79	19.72	
Shadow	121	91.3	86.78		0.76			
Non-shadow	121	87.4	91.74		0.89			
Object-based				88.43		0.77	18.69	
Shadow	121	89.74	86.78		0.76			
Non-shadow	121	87.2	90.08		0.89			

The categorization of canopy shadowiness based on a fuzzy logic showed that the majority of extracted features contained real canopy shadows. Overall, 78%-88% of sampled features in Yutsuntsa and 79%-89% of samples in Sawastian had real canopy shadow coverage in > 50% of the areas in extracted features (Table 6.3). Percentages of sampled features that contained real canopy shadows varied among different images in both Yutsuntsa and Sawastian, suggesting that the feature extraction effort and success might be uneven. Such unevenness could result from heterogeneous canopy structures and micro-habitats in the forests that caused different textures, colors, and spatial arrangement of canopy shadows.

Table 6.3. Percentage of sampled features that contained real canopy shadows in > 75%, 50-75%, 25-50%, and < 25% of the total area in each extracted feature.

		% area of sampled features			
Mosaic	Sample size	> 75%	50-75%	25-50%	<25%
Yutsuntsa					
A	118	54.24	25.42	14.41	5.93
B	110	47.27	30.91	13.64	8.18
C	105	61.9	24.76	8.57	4.76
D	124	53.23	31.45	9.68	5.65
E	72	48.61	34.72	9.72	6.94
F	110	57.27	28.18	8.18	6.36
G	91	54.95	30.77	7.69	6.59
H	101	50.5	37.62	6.93	4.95
I	80	53.75	30	11.25	5
Sawastian					
A	149	42.28	42.28	8.05	7.38
B	123	36.59	45.53	10.57	7.32
C	126	37.3	50	5.56	7.14
D	73	32.88	49.32	8.22	9.59
E	107	16.82	62.62	8.41	12.15

(Table 6.3 continued)

F	113	27.43	59.29	7.08	6.19
G	78	17.81	63.01	8.22	10.96
H	96	26.04	62.5	7.29	4.17
I	121	18.18	64.46	10.74	6.61

Landscape pattern metrics of canopy shadows

Patch abundance, size range, and distribution of canopy shadows can reflect part of forest dynamics and disturbance history as an indirect indicator of how natural and anthropogenic factors affect canopy structure. Canopy shadows showed various landscape properties in different areas of Yutsuntsa and Sawastian. There were 2,356-5,409 and 2,938-8,314 canopy shadows in each image in Yutsuntsa and in Sawastian, respectively. These canopy shadows accounted for 3.7%-6.6% of the area in each image in Yutsuntsa and 3.8%-8.1% in Sawastian (Table 6.4). The hemispheric photos taken within the three 1-ha plots (see Chapter 4) showed estimated 7.1%-8.5% of percentage canopy openness in Yutsuntsa, 6.2%-9.2% in Juyuintsa, and 7.1%-12% in Sawastian. Although hemispheric photos and aerial photographs were taken at different levels (bottom-up vs. top-down) and canopy shadow areas and percentage canopy openness were computed differently, these two methods suggested that average canopy opening/shadowiness ranged between 5%-10% in southeastern Ecuador. Density of canopy shadows also varied, from 5.9/ha to 13.5/ha in Yutsuntsa and from 7.4/ha to 20.8/ha in Sawastian. The average canopy shadow size did not differ greatly among different images in both Yutsuntsa and Sawastian (Table 6.4). Canopy shadows in both Yutsuntsa and Sawastian appeared to show much irregularity in shape according to the area weighted mean shape index. This index equals the sum of each shadow's perimeter, divided by the square root of shadow area, and divided by the number of shadows (Patch

Analyst Help). It increases from the value of one, at which the canopy shadows are circular. Hence, there appeared to be many vertices around the edges of the canopy shadows (Table 6.4). The high density of canopy shadows contributed to the short distances (5.2-9.2 m in Yutsuntsa and 4.8-7.4 m in Sawastian) between adjacent canopy shadows (Table 6.4).

Table 6.4. Landscape pattern metrics of canopy shadows in Yutsuntsa and Sawastian. The detailed metric definitions can be found in McGarigal and Marks (1994 and 1995) and Ritters et al. (1995).

Mosaic	Shadow area (ha)	Number of shadows	Shadow density (/ha)	Mean shadow size (m^2)	Area Weighted Mean Shape Index	Mean Nearest Neighbor Distance (m)
Yutsuntsa						
A	24.18	4112	10.28	58.84	2.39	7.79
B	23.29	4285	10.71	53.17	2.06	7.38
C	22.12	4558	11.40	48.46	2.28	7.37
D	26.47	4991	12.48	52.04	2.6	5.24
E	14.95	2356	5.89	63.49	2.21	8.84
F	23.18	4040	10.10	56.53	2.85	5.95
G	19	5409	13.52	34.62	2.42	5.45
H	21.34	3750	9.38	56.08	2.35	7.26
I	16.55	3011	7.53	55.07	2.2	9.23
Sawastian						
A	32.39	8314	20.79	36.63	2.53	4.86
B	26.3	5393	13.48	47.79	2.51	6.05
C	27.01	5305	13.26	50.79	2.36	6.67
D	15.14	4168	10.42	35.43	2.28	7.38
E	22.53	4859	12.15	45.39	2.4	6.17
F	23.99	4348	10.87	53.85	2.47	6.72
G	16.24	2938	7.35	54.25	2.29	6.09
H	21.01	5671	14.18	34.24	2.01	4.83
I	25.8	4600	11.50	55.49	2.58	5.79

Spatial patterns of canopy shadows

Spatial clustering and dispersion of canopy shadow sizes may reflect biotic and abiotic ecological processes that result in concentration or lack of concentration of large/small canopy shadows. Global and local spatial autocorrelation indices assist in identifying spatial clustering of canopy shadows. Global Moran's I, General G, and local Moran's I were computed for examining whether or not spatial clustering existed regarding size of canopy shadows and what kind of clustering pattern was present. The global Moran's I and General G of the area of the canopy shadows in all images for Yutsuntsa and Sawastian indicated spatial clustering and clustering of canopy openings in large size ($p < 0.05$ for all Z scores). Visual inspection of the clustered canopy shadows ($p < 0.05$) showed that the majority of the clustering occurred nearby or within palm swamps of *Mauritia flexuosa*, open shrubs and grasslands, and large rivers. Local Moran's I suggested that clustering of large canopy shadows surrounded by other large canopy shadows ($p < 0.05$ for Z scores) mostly occurred nearby or inside palm swamps in both Yutsuntsa and Sawastian. Clustering of small canopy shadows surrounded by other small canopy shadows, small canopy shadows surrounded by large canopy shadows, and large canopy shadows surrounded by small canopy shadows ($p < 0.05$ for Z scores) also occurred mainly in palm swamps in Sawastian, but spread extensively in Yutsuntsa.

Canopy palm distribution patterns

Canopy shadow extractions provided information regarding alpha diversity-level forest features. At a larger, regional scale, identifying palms and their spatial distribution could provide insights on beta diversity properties in respect of one of the most prominent and remotely discernible tree taxa in the Amazon. As an exploratory analysis, I identified and located 8,855 canopy palms of three species from 52 mosaicked aerial

photographs at a resolution of 5 cm. These aerial photographs were taken along multiple transect flight lines in the study region (see Chapter 3: Methods), but the coverage of these photographs did not overlap with the photomosaics of Yutsuntsa and Sawastian. Overall, *Socratea exorrhiza* was the most abundant species whereas *Mauritia flexuosa* was the least abundant (Table 6.5). *Mauritia flexuosa* only occurred in swamp forests in groups of multiple individuals, thereby showing the longest average distance to conspecific neighbors (Table 6.5). Both *Socratea exorrhiza* and *Oenocarpus bataua* were found in almost every aerial photograph. Given that the minimum distance to conspecific neighbors was very short for all three species, the palms appeared to occur in clusters (Table 6.5). Ripley's K function with ten distance classes for each species also revealed that the three palm species were spatially clustered over various distances. The very common and widely distributed *Socratea exorrhiza* and *Oenocarpus bataua* showed much lower average distance to a nearest neighbor of the same species compared to *Mauritia flexuosa*, which was only found in swamps (Table 6.5).

Table 6.5. Abundance, density, average distance to the nearest conspecific neighbor, and minimum distance to a conspecific neighbor for the three palm species.

Species	Abundance	Density (/ha)	Average distance to conspecific nearest neighbor (m)	Minimum distance to conspecific neighbor (m)
Mauritia flexuosa	274	0.6	392.81 m (clustered)	3.69
Oenocarpus bataua	1883	4.13	19.47 m (clustered)	2.63
Socratea exorrhiza	6698	14.69	10.56 m (clustered)	2.32

DISCUSSIONS

This dissertation employed object-based classification, as well as pixel-based and object-based accuracy assessment methods to extract canopy shadows out of aerial

photographs. The classification showed nearly or slightly over 90% producer's, user's, and overall accuracies according to both pixel- and object-based accuracy assessment approaches. Kappa statistics indicated that agreements between the references and classified features reached "substantial" to "almost perfect" levels. The accuracy assessment method that took a fuzzy logic approach also suggested that nearly or over 80% of extracted features covered over 50% area of real canopy shadows. Due to the lack of other high-resolution remote sensing data in the study region, this study took a novel approach of using the same sources for both input and reference images for accuracy assessment. Previous object-based classification studies had overlaid selected polygons for validation on the data used for classification (e.g. Grenier et al. 2008), but this dissertation study did not rely on any ancillary data to build an interpretation key. This approach yielded high accuracies that not only supported the object-based classification method, but also the accuracy assessment methods since they all reached an agreement of high classification accuracies.

This study showed that using pixel-based, object-based, or fuzzy logic-based sampling method for accuracy assessment is effective for object-oriented classifications. Researchers have the flexibility to choose the least time-consuming and labor-intensive method and yet retain high confidence in assessing classification accuracies. Furthermore, under the condition of unavailable reference data, any of these methods can still provide high accuracies when source and reference data come from the same imagery. A shortage of cloud-free and high-resolution remote sensing images is a persisting challenge in remote areas, especially in the wet tropics. Prior to using aerial photographs for forest feature extractions, I attempted to acquire high-resolution multispectral QuickBird images in the Yutsuntsa, Juyuintsa, and Sawastian communities. Unfortunately the rainy season from 2007-2008 resulted in many failed attempts of

cloud-free image acquisition. Therefore, launching a new task may result in a long waiting window and using archived data may be costly or misleading. Frequent rainfalls enhance difficulty in obtaining high-resolution images with the least cloud cover. My dissertation provides a unique solution by using the same images as references and inputs for accuracy assessment. This solution offers researchers great flexibility and confidence in accuracy assessment for analysis in remote locations.

A few studies aimed to extract and quantify canopy gaps or shadows by using remote sensing techniques for automated characterization of forest canopy properties (Foody et al. 2003, Koukoulas and Blackburn 2004, Plowes 2005, Asner et al. 2008, Hinsley et al. 2008, Morales et al. 2008). Foody et al. (2003) used maximum likelihood classification to extract gap properties from fine-resolution airborne imagery. Plowes (2005) integrated aerial photographs and Landsat images in a subpixel analysis to determine the likelihood of forest gaps in each pixel. Morales et al. (2008) used traditional pixel-based and new object-oriented classifications to classify tree shades and crown-shade transitions in IKONOS multispectral images. The majority of canopy gap characterization studies took advantage of the high resolution and vertical profile brought by the light detection and ranging (LiDAR) images to delineate and map gaps (Koukoulas and Blackburn 2004), to model canopy height and surfaces in order to mask out gaps and canopy shadows (Asner et al 2008), and to document canopy regeneration and disturbance regimes (Vepakomma et al. 2008). Among the abovementioned studies, only Vepakomma et al. (2008) took the object-based classification approach to delineate and study spatially extensive short-term dynamics of canopy gaps, in order to provide information on gap expansions, new gap openings, and gap closure due to lateral or vertical growth of adjacent vegetation.

Although my dissertation is not the first that used object-based classification techniques for canopy gap/shadow extraction, it serves as a pioneer for applying object-based classification on canopy gap/shadow extraction by using fine-resolution aerial photographs. Lacking multispectral information which provides spectral signals to facilitate distinguishing different forest features, feature extraction out of aerial photographs solely relies on color, texture, and spatial relationship among targeted objects. Furthermore, the 18 images used in this dissertation are mosaicked aerial photographs that were obtained along multiple flight paths, and were not color balanced during the mosaicking processes. Therefore, I faced a two-phased challenge to first reduce the effects of illumination and unbalanced colors, and then to develop the best feature extraction parameters. Phase one was based on trial and error in search of the best built-in filter, whereas phase two integrated trial and error, as well as recommendations from Miller et al. (2009). Both phases were successful during the data pre-processing stage, given that the classification accuracies were exceptional.

The object-based feature extraction in this study reached high accuracies that were comparable to some of the preceding work that reached very high classification accuracies. A tree species identification and classification study using IKONOS images reached 94% overall accuracy (Hájeck 2006). Yuan et al. (2008) and Zhou et al. (2008) documented land use land cover (LULC) changes with over 90% overall accuracies. Frohn et al. (2009) and Castillejo-Gonzalez et al. (2009) extracted wetland and agricultural features with over 85% accuracies, while Miller et al. (2009) and Zhou and Troy (2009) were able to respectively distinguish impervious vs. pervious and trees vs. disturbance features with over 90% overall accuracies. The majority of these object-based classification studies used multispectral images, unlike this dissertation research in which the extractions were derived from aerial photographs. Extracting features from aerial

photographs is more challenging than using multispectral imagery because the training samples do not contain spectral signals that can contribute to a reference library. Therefore, this aerial photograph-based canopy shadow extraction performed exceptionally well despite the two-phase challenge described above.

This dissertation project and most up-to-date canopy studies in remote sensing have focused on extracting canopy crowns or canopy gaps (e.g. Erikson et al. 2004, Couteron et al. 2005, Greenberg et al. 2005, Bunting and Lucas 2006), estimating canopy properties and heterogeneity (Clark et al. 2004a, Song et al. 2007, Asner et al. 2008, Palace et al. 2008, Barbier et al. 2010), and relating canopy metrics to field-based ecological data (e.g. Clark et al. 2004b, Chubey et al. 2006). An emerging but not widely studied topic is individual tree species identification in remote sensing. Attempts have been made with statistical detection (Foody et al. 2005), image segmentation (Hájeck 2006), and object-oriented extraction (Bunting and Lucas 2006, Leckie et al. 2005). Identifying and extracting individual tree species requires a priori knowledge of canopy and emergent trees based on either field inventories with highly accurate tree locations, or an analyst's capability of identifying tree species in fine-resolution remote sensing images.

The difficulty increases exponentially in the wet tropics, given that it is challenging to obtain cloud-free fine-resolution images, to find inventory plots/transects where high-resolution remote sensing data are also available, and to encounter a situation in which an analyst is able to identify diverse tree species from remote sensing images. In one of the very few tropical studies, Clark et al. (2005) used hyperspectral data to differentiate seven emergent tree species in Costa Rica by comparing spectra at leaf, pixel, and crown scales. Originally I ordered QuickBird images for species-level classification studies in the Ecuadorian Amazon, but the task failed after over six months

of unsuccessful attempts to record cloud-free imagery. Unfortunately the three tree inventory plots (Yutsuntsa, Juyuintsa, and Sawastian) were not covered by the aerial photographs and still images at 10-cm and 5-cm resolutions, respectively, and an expert botanist was unable to identify even tree families based on aerial photographs. Using Feature Analyst to extract palm trees in my preliminary analysis was unsuccessful due to the difficulty in extracting umbrella-like unique palm canopies. I argue that with the combination of thorough field inventories and fine-resolution images (multispectral or preferably hyperspectral), object-based tree identification can be feasible in the tropics. The results of object-based classifications can provide density- and species richness-related information after identifying the respective spectral information of certain species groups. Future research should examine spatial variation in vegetation indices, tree density, number of species, species diversity estimates, and species distribution of emergent and canopy trees detected in remote sensing imagery. Spatial variation in imagery-derived tree diversity patterns should reflect the spatial heterogeneity of local vegetation and habitat types. To facilitate alpha diversity studies in the remote tropics and to complement ground-based tree diversity and distribution research in order to enrich the understanding for conservation biogeography, this aerial-based approach at a very fine resolution and improvement of relevant techniques should continue to be explored in future research.

From alpha diversity patterns to beta diversity understandings, using remote sensing to examine tree diversity and distribution in the species-rich Amazon remains a challenge. In this dissertation I sought to identify palms from remote sensing data as an exploratory analysis because palms represent unique and prominent canopy taxa in the Neotropics, and they were shown to be important the diversity studies of this dissertation (see Chapters 4 and 5). Without any availability of QuickBird images or success of

feature extraction of palm canopies, using high-resolution aerial photographs for palm demography and exploratory spatial distribution studies provided information that complemented ground inventories. Both *Oenocarpus bataua* and *Socratea exorrhiza* also occurred in 1-ha plots in Yutsuntsa, Juyuintsa, or Sawastian. This study aided in documenting the changing density of *Oenocarpus bataua* and *Socratea exorrhiza* over the landscape and suggested a potential gradient of abundance for common palm species in the Ecuadorian Amazon.

In addition, I propose that spatial point pattern analysis and spatial associations between palm individuals (identified and documented as points) in aerial photographs should be conducted in future research. Similar to the global, local, and bivariate spatial analyses employed for the alpha diversity study presented in Chapter 4, examining spatial point patterns and spatial associations of palms may shed light on intraspecific and interspecific relationships of palms, as well as forest dynamics or disturbance history. Furthermore, the importance of canopy palms in forest structure, dynamics, and recruitment has been examined in multiple studies (e.g. Farris_Lopez 2004, Vormisto et al. 2004, Wang and Augspurger 2004, 2006). The aforementioned inventory plots provided one of the first floristic descriptions in southeastern Ecuador, but large-scale ground inventories are not feasible in this region due to the remoteness and costly field labors. Using high-resolution aerial photographs to conduct rapid inventories of canopy trees that are identifiable and discernible aids to the understanding of the spatial variation in species diversity patterns in unknown areas. Extracting palm diversity and distribution out of aerial photographs helps to fill the gap in forest community studies. More aerial photographs have been taken in southeastern Ecuador (R. Sierra, unpublished data) since the data analysis was conducted. Therefore, conducting more rapid "aerial" inventories of

palms will complement current ground plots and facilitate answering some of the alpha or beta diversity questions discussed in the previous dissertation chapters.

However, manual identifying and locating canopy trees from high-resolution images can be laborious and time-consuming. Adopting a repeatable remote sensing technique that allows users to automate processes of canopy or species recognition is an ideal approach. With the improvement of resolution in multispectral imagery, studies that estimate biodiversity by discriminating tree leaves, crowns or other taxonomic characters began to emerge (Fabbro 2001, Asner et al. 2002a, Read et al. 2003, Clark et al. 2004a, Clark et al. 2004c, Clark et al. 2005). In terms of distinguishing species composition and habitat heterogeneity, similarities in spectral reflectance patterns in remote sensing imagery were found to be highly correlated to similarity patterns in floristic and edaphic variables (Tuomisto et al. 2003a, Tuomisto et al. 2003b). For example, with an object-based classification, QuickBird images were useful in detecting targeted plant individuals, calculating stem density, and presenting gradients of land use (Laliberte et al. 2004, Ivits et al. 2005). At the population level, QuickBird predicted landscape-scale annual exponential death rate of tropical forest trees (Clark et al. 2004b). At the community level, the spectral heterogeneity of visible and infrared bands explained variance in species richness at different scales (Rocchini et al. 2004). Future research can use aerial photographs as references to assist assessing the accuracy of analyzing high-resolution multispectral images. At the species level, emergent and canopy tree species with distinct crown characteristics (e.g. palms and deciduous tree species) can be identified and located for predictions of species abundance and species richness (Hess et al. 2002, Hess et al. 2003, Powell et al. 2004). By extracting spectral information of these species in the red/infrared bands from high-resolution multispectral images (e.g.

QuickBird), tree density, number of species, and species diversity of emergent and canopy trees may be estimated.

In addition, examining whether or not the products of two exploratory analyses (canopy shadows and palms) based on aerial photographs are associated with each other can be included in future research because both canopy gaps/openings and palms are important properties in tropical forests. Clusters of the canopy shadows extracted in this study were often found nearby palm swamps, suggesting that there may be spatial associations between canopy gaps and palms. Canopy features and palms may be indicative of some aspects of the overall forest structure and dynamics. I conducted an exploratory analysis to examine if density of palms was associated with size of canopy shadows, type of spatial cluster of canopy shadows, or the combination of both. I conducted a stratified random selection to choose canopy shadows that were considered spatial clusters in their size according to local Moran's I. Twenty-five samples in each cluster type were chosen for each aerial photograph: large canopy shadows surrounded by other large canopy shadows (High-High clusters), small canopy shadows surrounded by other small canopy shadows (Low-Low clusters), small canopy shadows surrounded by large canopy shadows (Low-High clusters), and large canopy shadows surrounded by small canopy shadows (High-Low clusters). I then visualized and counted all the palms within a buffer zone of 50-m radius from the edge of each selected canopy shadow. A preliminary analysis of variance (ANOVA) indicated that the clustering type of canopy shadows ($F = 5.7$, $p < 0.05$) and the cluster type with canopy shadow size as a covariate ($F = 4.9$, $p < 0.05$) had significant effects on number of palms in one aerial photograph. This occurred in Sawastian, where palms were more abundant around small canopy shadows that were surrounded by other small canopy shadows (Pearson's $r = 0.29$), and large canopy shadows surrounded by small canopy shadows (Pearson's $r = 0.23$).

Further spatial analyses are necessary to verify whether or not these three palm species are associated with particular clusters of canopy shadows, in order to complement other palm studies that examined how palms response to canopy gaps or general disturbances. The development of arborescent palms is partially determined by light reaching the understory (Kahn 1986). Although palms are generally recognized as shade-tolerant species, certain palms behave as opportunists for recruitment after gap formation, such as some species in *Geonoma* and *Oenocarpus* (Svenning 1999, Rodriguez-Buritica et al. 2005, Yepes et al. 2010). With the ability to take advantage of deforestation, palms can become more abundant and dominant in secondary vegetation (Pintaud 2006). With strong temporal and spatial random variation in the physical environment promoted by gap formations, canopy gaps can facilitate release of suppressed seedlings (Martinez-Ramos et al. 1988).

However, unlike the observation by Zimmerman and Covich (2007) that palms are not affected after a hurricane, not all palm species are unaffected by sun exposure after major disturbances. Growth and survival of *Iriartea*, for instance, are not dependent on gaps (Svenning 1999). Baez and Balslev (2007) found that adult palm density and species richness decrease towards edges of forest fragments, showing negative effects of disturbances. Svenning (1998) also discovered that although different palms respond to different levels of anthropogenic disturbances, species richness of palms maximize in undisturbed forests. Since palms appear to be indicative of some aspects of forest dynamics in their various responses to canopy gap formation, I propose to integrate palm community studies into future canopy gap research by using remote sensing methods. The advantage of studying the association between palm communities and canopy gap dynamics is that palms are visually discernible and distinguishable from other tropical tree species in fine-resolution images. As techniques of palm crown and canopy gap

extractions continue to advance, shifting palm diversity and distribution studies from a traditional ground-based to a fine-resolution, remote sensing-based approach can provide greater efficiency in ecological research.

Chapter 7: Landscape zonation map design in southeastern Ecuador

RESULTS

Remote sensing-based habitat mapping

Habitat classification

Conservation biogeography seeks to apply understandings of biodiversity patterns to practical conservation planning. Two primary biodiversity components, alpha and beta diversity features, are constituents of heterogeneous land cover types. Therefore, broad-scale biodiversity conservation requires information regarding landscape covers that represent alpha and beta diversity at a coarse scale. In this chapter I first present the result and accuracy assessment of habitat classification that was derived from object-based classification using pan-sharpened Landsat ETM+ images at a 15-m resolution. I then compare two landscape zonation maps based on a people- vs. a biodiversity-oriented approach. Both approaches used habitat classes and other remote sensing-derived and GIS data.

Lowland evergreen forests on hilly terrain, flat terrain, and in white water areas, as well as palm swamps, accounted for over 92% of the study area in the Ecuadorian Amazon (Figure 7.1, Table 7.1). As the most dominant habitat type, lowland evergreen forests on hilly terrain were present in 53% of the landscape, followed by lowland evergreen forests on flat terrain (Table 7.1). A new class, lowland evergreen forests on mixed terrain was added during the hierarchical learning process of classification due to its unique features that combined the characteristics of lowland evergreen forests on both flat and hilly terrain (Figure 7.1, Table 7.1). This class was only found in the northwestern part of the study region. Lowland evergreen forests in white water areas and palm swamps respectively occurred in less than 10% of the study region near large rivers.

Shrub and grass vegetation occurred in small clusters of patches and was found occasionally (Table 7.1). The rare secondary forests and human land use habitats were only found in areas within or adjacent to indigenous communities. Upper lowland evergreen forests on hilly terrain were only found at the northwestern corner of the study region (Figure 7.1).

Figure 7.1. Object-based habitat classification in the study area, as the classification results of four Landsat images (the lower right corner).

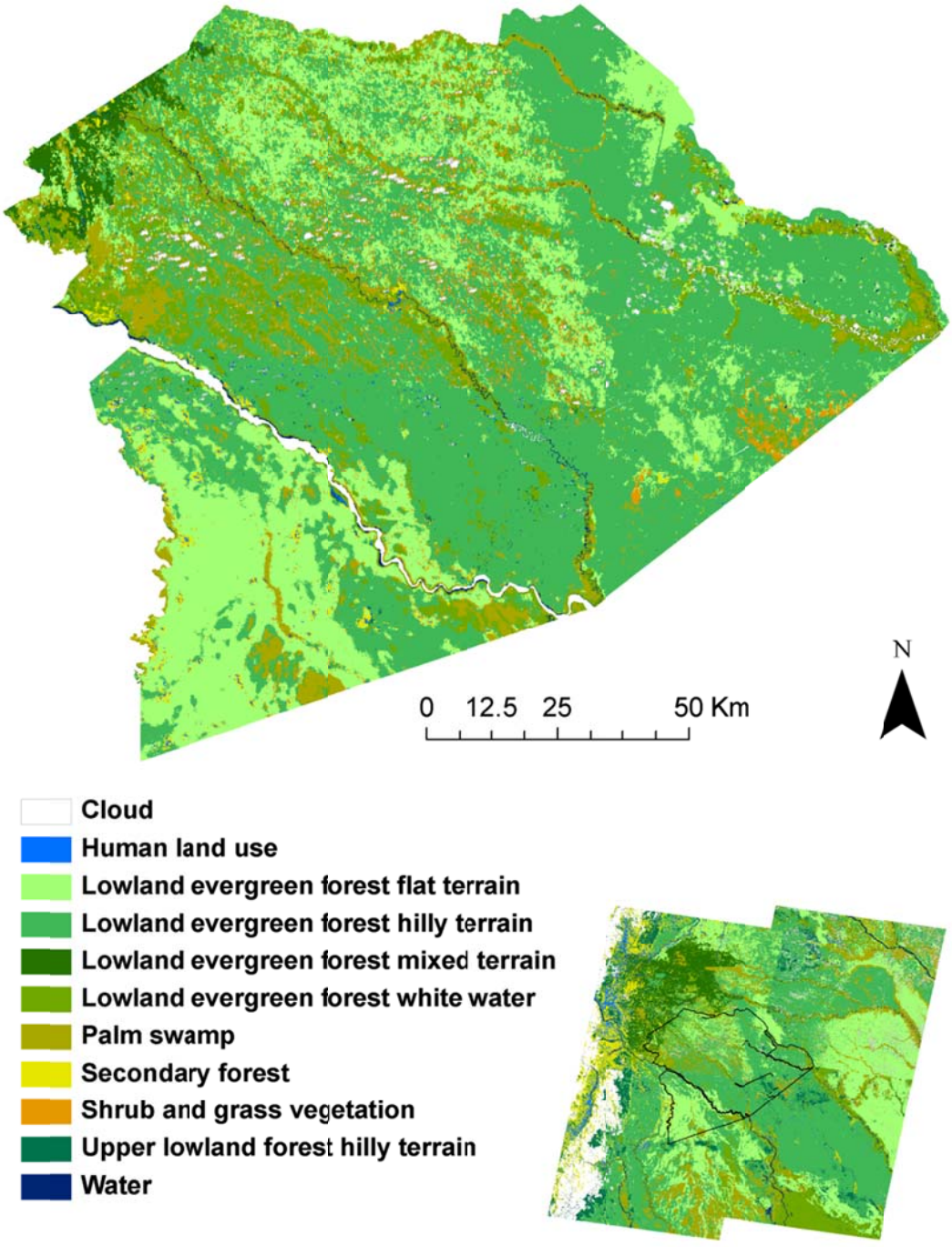


Table 7.1. Total area and percentage cover of each habitat type in the study region.

Class	Total area (km^2)	Percentage area (%)
Lowland evergreen forest on hilly terrain	9549.08	53.04
Lowland evergreen forest on flat terrain	4173.39	23.18
Lowland evergreen forest in white water	1667.60	9.26
Palm swamp	1319.60	7.33
Shrub and grass vegetation	475.22	2.64
Cloud	228.24	1.27
Lowland evergreen forest on mixed terrain	214.56	1.19
Secondary forest	162.56	0.90
Water	93.79	0.52
Upper lowland forest on hilly terrain	74.28	0.41
Human land use	46.05	0.26

Accuracy assessment of the object-oriented habitat classification

The original classification used ten classes (including cloud) to delineate training samples. During the hierarchical learning processes of classification for identifying correctly and incorrectly extracted landscape features, I noticed two large polygons with mixed spectral, textural, and spatial information that could not be classified into any of the existing classes. Therefore, a new class of lowland evergreen forest on mixed terrain was added into the classification scheme. The accuracy assessment, however, only consisted of nine classes with sufficient areas and number of polygons to sample from.

Overall, both pixel-based and object-based sampling methods indicated similar levels of producer's, user's, and overall accuracies. For pixel-based sampling, the producer's accuracy had an average of 83.39% with a range from 54.12% (lowland evergreen forests on hilly terrain) to 100% (shrub and grass vegetation, upper lowland evergreen forests on hilly terrain). The user's accuracy showed an average of 78.38% with a range from 69.09% (shrub and grass vegetation) to 89.09% (human land use)

(Table 7.2). The overall accuracy was 78.38%. The conditional Kappa statistics (K_{hat}) for individual classes were between 0.67-0.88 with an average of 0.76, indicating a "substantial" to "almost perfect" agreement between classified and reference data according to the interpretation of Kappa statistics provided by Ladis and Koch (1977) (Table 7.2). Z statistics exceeded the threshold value of 1.96 at a 95% confidence interval, suggesting that the classifications were much better than random placement of pixels (Table 7.2).

The object-based sampling had producer's accuracies comparable to the pixel-based sampling, with an average of 83.91% within a range of 57.32% (lowland evergreen forests on hilly terrain) to 100% (shrub and grass vegetation, upper lowland evergreen forests on hilly terrain) (Table 7.2). Likewise, the user's accuracies showed minimum (67.27% for shrub and grass vegetation), maximum (90.91% for water), and average (79.8%) values that were similar to the pixel-based sampling method (Table 7.2). The conditional Kappa statistics (K_{hat}) ranged between 0.65-0.9, indicating a "substantial" to "almost perfect" agreement between classified and reference data according to Ladis and Koch (1977) (Table 7.2). Z statistics exceeded the threshold value of 1.96, showing that the classifications were much better than random pixel placement (Table 7.2). The Z score between the two error matrices of pixel- vs. object-based samplings was not significant at a 95% confidence interval (Table 7.2). In summary, both accuracy assessment sampling methods consistently showed that that the classifications of lowland evergreen forests on flat and hilly terrain obtained the lowest producer's accuracies, whereas human land use and water classes obtained the highest producer's and user's accuracies (Table 7.2).

Table 7.2. Summary of producer's accuracy, user's accuracy, overall accuracy, conditional and overall Kappa statistics (K_{hat}), and Z statistics of two sampling methods of accuracy assessment using pixel-based and object-based approaches.

Class	Producer's accuracy (%)	User's accuracy (%)	Overall accuracy (%)	Conditional K_{hat}	Overall K_{hat}	Z score
Pixel-based sampling						
Human land use	98.00	89.09		0.88		
Lowland evergreen forest on flat terrain	60.00	81.82		0.79		
Lowland evergreen forest on hilly terrain	54.12	83.64		0.80		
Lowland evergreen forest in white water	63.64	76.36		0.73		
Palm swamp	81.48	80.00		0.78		
Secondary forest	97.56	72.73		0.70		
Shrub and grass vegetation	100.00	69.09		0.67		
Upper lowland evergreen forest on hilly terrain	100.00	70.91		0.68		
Water	95.74	81.82		0.80		
			78.38		0.76	36.38*
Object-based sampling						
Human land use	100.00	85.45		0.84		
Lowland evergreen forest on flat terrain	57.89	80.00		0.76		
Lowland evergreen forest on hilly terrain	57.32	85.45		0.83		
Lowland evergreen forest in white water	74.58	80.00		0.77		
Palm swamp	81.48	80.00		0.78		
Secondary forest	91.30	76.36		0.74		
Shrub and grass vegetation	100.00	67.27		0.65		

(Table 7.2 continued)

Upper lowland evergreen forest on hilly terrain	100.00	72.73		0.70		
Water	92.59	90.91		0.90		
			79.80		0.77	38.08*
Z score between two matrices	0.55					

Both pixel-based and object-based samplings presented similar patterns of misclassification for different landscape features. For instance, six out of 55 features of classified lowland evergreen forests on flat terrain were actually lowland evergreen forests on hilly terrain. Some features of lowland evergreen forests in white water and on flat terrain were misclassified as features of lowland evergreen forests on hilly terrain (Table 7.3). Some of the classified palm swamps included actual lowland evergreen forests on flat and hilly terrain. Secondary forests, shrub and herb vegetation, and upper lowland evergreen forests on hilly terrain contained fewer misclassified landscape features (Table 7.3). Classes of human land use and water had the least misidentified landscape features. Overall, both pixel-based and object-based sampling methods captured that lowland evergreen forests shared some features with mixed spectral, textural, and spatial information that became more easily misclassified than other features. For instance, some features of palm swamps, shrub and herb vegetation, and upper lowland forests on hilly terrain were misidentified as lowland evergreen forests. Forests on flat vs. on hilly terrain could also easily confuse the classifier (Table 7.3).

Table 7.3. Error matrices based on pixel-based (A) and object-based (B) samplings for accuracy assessment, showing the number of correctly vs. incorrectly classified samples.

A.

	Reference									
	Human land use	Lowland evergreen forest on flat terrain	Lowland evergreen forest on hilly terrain	Lowland evergreen forest in white water	Palm swamp	Secondary forest	Shrub and herb vegetation	Upper lowland evergreen forest on hilly terrain	Water	Row total
Classified Human land use	49	3	1	2	0	0	0	0	0	55
Lowland evergreen forest on flat terrain	0	45	6	1	3	0	0	0	0	55
Lowland evergreen forest on hilly terrain	0	4	46	3	2	0	0	0	0	55
Lowland evergreen forest in white water	0	3	9	42	1	0	0	0	0	55
Palm swamp	0	2	7	2	44	0	0	0	0	55
Secondary forest	0	7	2	5	1	40	0	0	0	55
Shrub and herb vegetation	1	5	8	2	0	1	38	0	0	55

(Table 7.3 continued)

Upper lowland evergreen forest on hilly terrain	0	5	5	3	1	0	0	39	2	55
Water	0	1	1	6	2	0	0	0	45	55
Column total	50	75	85	66	54	41	38	39	47	495

B.

	Reference									
	Human land use	Lowland evergreen forest on flat terrain	Lowland evergreen forest on hilly terrain	Lowland evergreen forest in white water	Palm swamp	Secondary forest	Shrub and herb vegetation	Upper lowland evergreen forest on hilly terrain	Water	Row total
Classified Human land use	47	0	0	3	2	2	0	0	1	55
Lowland evergreen forest on flat terrain	0	44	8	1	1	0	0	0	1	55
Lowland evergreen forest on hilly terrain	0	3	47	3	1	1	0	0	0	55
Lowland evergreen forest in white water	0	4	6	44	1	0	0	0	0	55

(Table 7.3 continued)

Palm swamp	0	6	2	2	44	1	0	0	0	55
Secondary forest	0	4	5	3	1	42	0	0	0	55
Shrub and herb vegetation	0	9	7	2	0	0	37	0	0	55
Upper lowland evergreen forest on hilly terrain	0	4	7	0	2	0	0	40	2	55
Water	0	2	0	1	2	0	0	0	50	55
Column total	47	76	82	59	54	46	37	40	54	495

Landscape pattern metrics of classified habitats

Comparing landscape pattern metrics that are derived from different land cover types may demonstrate variation in landscape patch patterns among habitats, which may result from anthropogenic factors or ecological processes that structured landscape-level biodiversity features. The study area mainly consisted of lowland evergreen forests on flat and hilly terrain and in white water, as well as palm swamps (Table 7.4). These four vegetation types accounted for 69.3% of total number of classified features and 92.8% of total landscape area. Most habitat types comprised many features of 5-10 ha in size (Table 7.4). Area weighted mean shape index equals the sum of each feature's perimeter, divided by the square root of feature area, and divided by the number of features (Patch Analyst Help). This index increases from the value of one, at which the features are circular. Features of classes in human land use, shrub and herb vegetation, and upper lowland forests on hilly terrain had the lowest mean shape index, suggesting that their feature shape had greater regularity than other habitat types (Table 7.4). Human land use and shrub and herb vegetation had the lowest shape complexity because villages and clearings were constructed with regular shapes. Shrub and herb vegetation often occurred in small and nearly circular patches. These patches are discernible from Landsat images, but the ecological cause of their nearly circular shape remains unknown (S. Lopez, personal communication). Lowland evergreen forests on flat, hilly, and mixed terrain showed the greatest feature shape irregularity (Table 7.4). Area weighted mean fractal dimension approaches one for shapes with simple perimeters and approaches two when shapes are more complex (Patch Analyst Help). All habitat types shared a similar degree of shape complexity because their area weighted mean patch fractal dimension values were similar (Table 7.4). Shannon's index of feature diversity was 1.4. This index equals

zero when there is only one feature type in the landscape and increases as proportional distribution of feature types increases (Patch Analyst Help). Shannon's evenness index equals zero when the observed feature distribution is low and approaches one when the distribution of feature types becomes more even (Patch Analyst Help). Shannon's evenness index was 0.6 in this study.

Table 7.4. Landscape pattern metrics for each classified habitat type at the landscape level.

Class	Number of features	Area (ha)	Mean feature size (ha)	Median feature size (ha)	Mean shape index	Mean feature fractal dimension
Human land use	540	4602.6	8.5	6.0	2.9	1.4
Lowland evergreen forest on flat terrain	6289	417268.4	66.3	6.9	27.9	1.5
Lowland evergreen forest on hilly terrain	4804	954848.8	198.8	7.4	33.8	1.5
Lowland evergreen forest in white water	4723	166711.6	35.3	9.8	7.0	1.4
Palm swamp	4365	131909.1	30.2	8.9	7.4	1.4
Secondary forest	1050	16241.9	15.5	6.6	5.0	1.4
Shrub and herb vegetation	4661	47432.3	10.2	7.0	3.8	1.4
Upper lowland forest on hilly terrain	1003	7411.3	7.4	5.0	4.1	1.4
Water	360	9363.4	26.0	7.5	13.9	1.5
Lowland evergreen forest on mixed terrain	2	21455.7	10727.8	10727.8	35.1	1.5
Cloud	1331	22816.4	17.1	7.7	3.5	1.4
Total landscape	29128	1800061.5	61.8	7.5	26.3	1.5

Zonation map design

As a preliminary step prior to designing conservation area networks, creating a zonation map using land cover types and environmental features that harbor biodiversity components facilitates drawing a sketch of the importance of landscape properties in respect to spatially explicit criteria. The applied aspect of conservation biogeography can draw from future conservation area networks that are designed from zonation maps and additional emphasis on local needs and opinions. The ConsNet search performances showed that all individual targets for all classes of the topographic, vegetation, hydrological, and edaphic features were met. The selections (i.e. the number of grid cells selected by ConsNet) were all equal to or slightly more than the original targets for both biodiversity- and people-oriented approaches (Table 7.5). The northern side of the study area is less inhabited and utilized by indigenous communities, and thereby was considered as a preferred region to be included in zonation maps. ConsNet searches did not add this region as a preferred site into the objectives because the addition resulted in poor solutions in a preliminary analysis, but the selection of this region still increased as targets increased from 10% to 40% (Table 7.5).

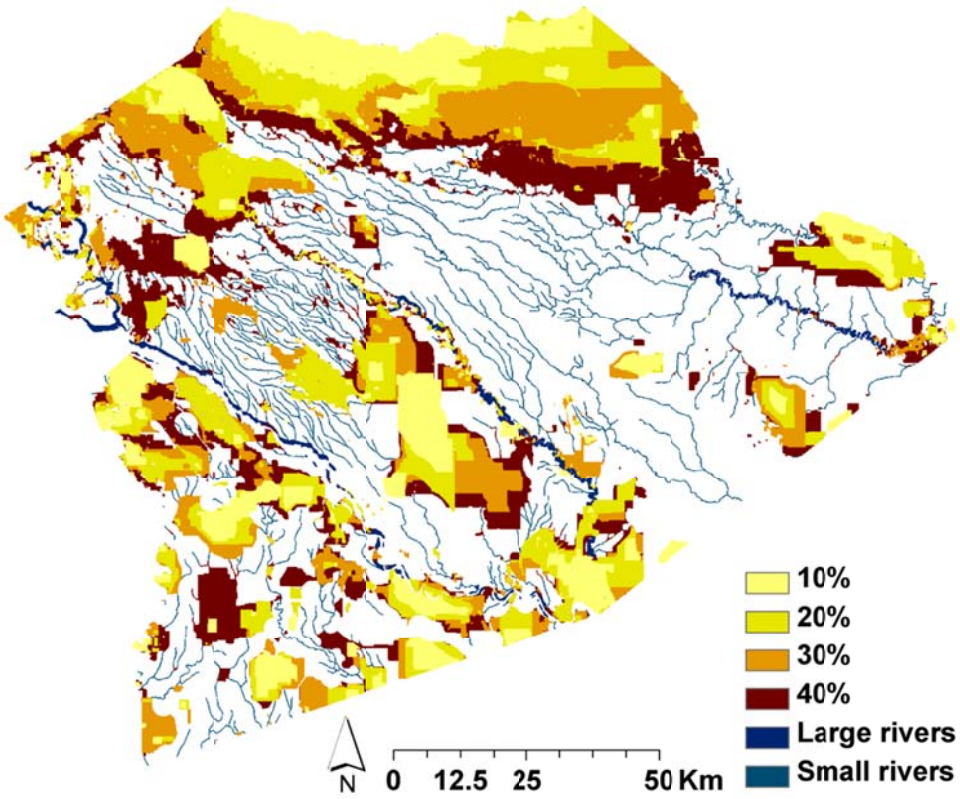
Visual inspection of the zonation map for the people-oriented approach indicated that when the target increased from 10% to 20%, most of the newly selected areas were connected to the previously chosen areas. Approximately 41.2% of areas (1,277 km^2) selected under the 20% target overlapped with the 10% target. Only a few small and relatively isolated patches were added to the selection according to the 20% target (Figure 7.2A). Similarly, except for a few medium-size newly selected areas that were not connected to the previous selections, large areas of selection under the 30% target were adjacent to the selection under the 20% target. There was a 61% (2,834 km^2)

overlap between areas selected under both targets (Figure 7.2A). However, when the target increased from 30% to 40%, despite the 63% (4,235 km^2) overlap in selected areas between the two targets and connections between large previously selected and newly added areas, many small and disconnected patches were shown near the northwestern part of the study area (Figure 7.2A).

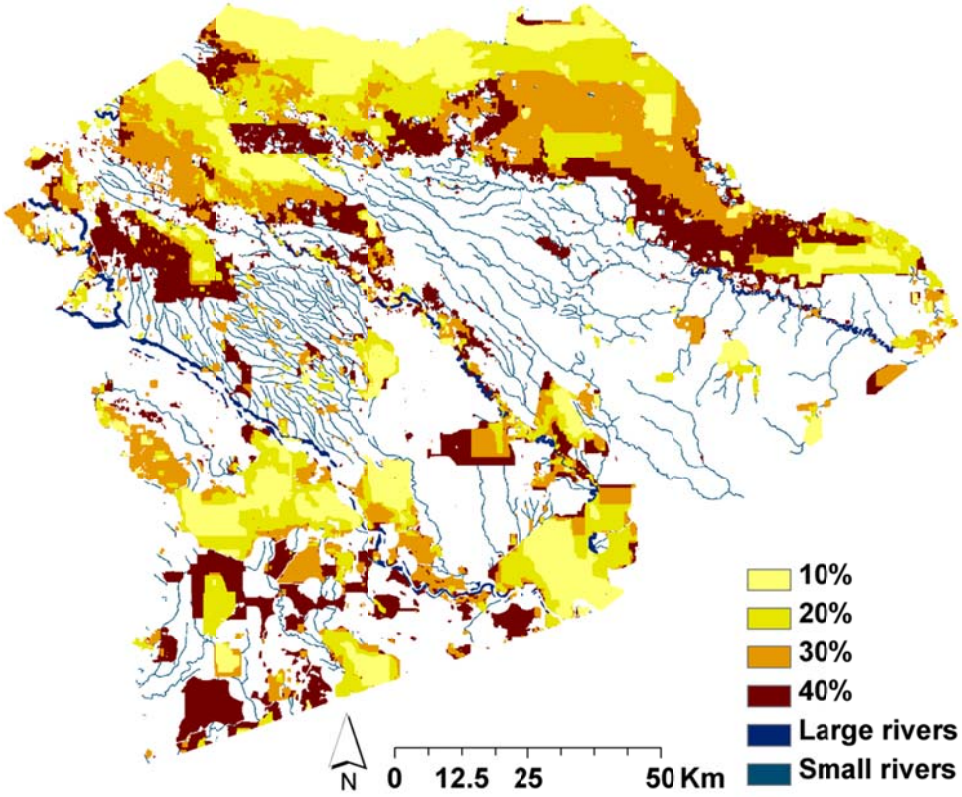
For the biodiversity-oriented approach, despite a few small-size areas that were selected under the 20% target and were relatively isolated, adjacency between areas selected under the 10% vs. 20% targets was observed (Figure 7.2B). Forty-one percent (1,284 km^2) overlap in selected areas existed between the two targets. When the target increased from 20% to 30%, however, many small to medium patches that were not connected to the previous selected began to appear. With a 60% (2,774 km^2) overlap between selections under the 20% and 30% targets, those isolated patches mainly occurred in the centeral and western parts of the study area (Figure 7.2B). At the 40% target, many more small and isolated areas were selected, especially near the rivers. There was a 67% (4,179 km^2) overlap between selections under the 30% and 40% targets, but overall the connection between newly selected vs. previously selected areas was poor (Figure 7.2B). By comparing the two zonation maps, the people-oriented approach showed visually discernible better performance than the biodiversity-oriented approach. In the following section I compare the two approaches in terms of their spatial characteristics.

Figure 7.2. Zonation maps showing selected areas by the 10%, 20%, 30%, and 40% targets based on the people-oriented (A) and biodiversity-oriented (B) approaches. See Figure 7.3 for areas of community centers and trails.

A.



B.



Overall, the people-oriented approach for the 10%, 20%, 30%, and 40% targets consistently showed greater compactness than the biodiversity-oriented approach. Shape or compactness, commonly measured as the perimeter to area ratio, is an important property because planners often wish to minimize the exposed perimeter while maximizing the enclosed area because edge effects may increase the vulnerability of biota (Ciarleglio et al. 2009). After converting the ConsNet outputs from centers of grid cells into polygons, the biodiversity-oriented approach contained 1.2-1.7 times more polygons than the people-oriented approach when the total area of polygons did not differ much between the two approaches (Table 7.6). Mean polygon size of based on the people-oriented approach was 1.2-1.7 times larger than the biodiversity-oriented

approach, whereas its total perimeter was smaller (Table 7.6). Mean perimeter-area ratio, mean shape index, and mean cluster fractal dimension of the people-oriented approach were all smaller than the biodiversity-oriented approach, indicating greater compactness and a simpler shape (Table 7.6). Polygons that were derived from the people-oriented approach showed greater mean distance to the nearest polygons than the biodiversity-oriented approach, suggesting that spatially the latter formed more small isolated patches across the landscape (Table 7.6).

Percentages of different land feature types among the total selected grid cells showed strong consistency in both the biodiversity- vs. people-oriented approaches for the 10%, 20%, 30%, and 40% targets. The northern side of the study area was defined as a preferred region for designing a zonation map, but was not included in the searches (see above). Percentage of selected grid cells that fell inside the northern side decreased as the target size increased, from 42% to 25% when the target increased from 10% to 40% using the biodiversity-oriented approach (Table 7.7). Similarly, the percentage dropped from 38% to 25% as the target size increased for the people-oriented approach. For topography, lowland flat areas (at least 63% of low elevation and 93% of gentle slopes) dominated the zonation map selections (Table 7.7).

For vegetation type, the biodiversity-oriented approach selected 15% more of lowland evergreen forests on flat terrain than the people-oriented approach. The people-oriented approach selected 9% more of lowland evergreen forests on hilly terrain, 2% more of lowland evergreen forests in white water areas, and 3% more of palm swamps than the biodiversity-oriented approach (Table 7.7). The difference in proportion of selected grid cells among different vegetation types between the two approaches reflected patterns of the relative weights in Table 3.2 that were used to determine individual targets. In terms of hydrology, 97% and 87% of the selections occurred outside the 200-m

and 100-m buffers of large and small rivers, respectively. Forty-three percent and 47% of the selections were within the respective Tigre and Pastaza River basins (Table 7.7). Soil type H1, Inceptisol Tropept soils, soil type F, and soil type K were the most dominant edaphic characteristics of the selected areas in zonation maps (Figure 2.11) (Table 7.7).

Table 7.5. Comparisons between number of grid cells in individual targets vs. selections regarding major land feature types. See Figure 2.11 for soil type identification.

Biodiversity-oriented	10% target		20% target		30% target		40% target	
Land feature type	Target	Selection	Target	Selection	Target	Selection	Target	Selection
Northern side (preferred)	0	44767	0	84426	0	94594	0	107395
Elevation 158-338 m	71834	71835	143668	143690	215502	215507	287336	287337
Lowland evergreen forest flat terrain	41538	41540	83076	83077	124614	124615	166152	166153
Lowland evergreen forest hilly terrain	42622	42624	85245	85246	127867	127868	170490	170491
Lowland evergreen forest white water	7971	7973	15943	15944	23914	23916	31886	31891
Palm swamp	9353	9355	18706	18707	28059	28060	37412	37413
Outside large river 200m buffer	102485	104601	204971	209196	307456	313790	409941	418383
Outside small river 100m buffer	95587	95588	191174	191422	286761	288184	382349	388893
Slope 0-12 degrees	100486	100488	200973	203475	301459	305632	401945	408833
Soil type H1	31195	31196	62391	62391	93586	93586	124781	124783
Soil type F1	9912	9991	19825	19844	29737	29740	39650	39677
Soil type F2	12933	12934	25866	25866	38799	38799	51731	51733
Inceptisol Tropept soil	13643	13653	27286	27291	40929	43029	54572	58087
Soil type K	7116	7117	14232	14232	21347	21349	28463	28465
Soil type K3	9771	9773	19543	19543	29314	29316	39086	39087
Tigre Basin	47210	47213	94419	94446	141629	145014	188838	193358
Pastaza Basin	51165	51166	102330	102331	153496	153496	204661	204661

(Table 7.5 continued)

People-oriented	10% target		20% target		30% target		40% target	
Land feature type	Target	Selection	Target	Selection	Target	Selection	Target	Selection
Northern side (preferred)	0	40298	0	82956	0	96980	0	108093
Elevation 158-338 m	68137	68139	136275	136276	204412	204413	272550	273113
Lowland evergreen forest flat terrain	25419	25422	50839	50840	76258	77490	101677	102583
Lowland evergreen forest hilly terrain	52166	52166	104331	104800	156497	156498	208663	208663
Lowland evergreen forest white water	9756	10307	19513	19514	29269	29337	39025	39027
Palm swamp	12719	12720	25438	25440	38158	38159	50877	50877
Outside large river 200m buffer	102485	104601	204971	209196	307456	313790	409941	418383
Outside small river 100m buffer	95587	97704	191174	195400	286761	293095	382349	390791
Slope 0-12 degrees	99708	99839	199415	201857	299123	304254	398831	407019
Soil type H1	29162	29164	58324	58327	87486	87487	116648	116650
Soil type F1	9266	9374	18533	22186	27799	29742	37066	37077
Soil type F2	12090	12090	24180	24181	36270	36271	48360	48360
Inceptisol Tropept soil	12754	14715	25508	25509	38262	41710	51015	56642
Soil type K	6652	6652	13304	13305	19956	19957	26608	26609
Soil type K3	9135	9136	18269	18369	27404	27405	36538	36539
Tigre Basin	46465	46465	92929	92930	139394	140790	185859	190068
Pastaza Basin	50358	50358	100716	100716	151074	151074	201432	201432

Table 7.6. Summary of the best solutions for the 10%, 20%, 30%, and 40% targets using biodiversity- and people-oriented approaches.

	10% target		20% target		30% target		40% target	
	Biodiversity	People	Biodiversity	People	Biodiversity	People	Biodiversity	People
Number of polygons	225.00	147.00	304.00	255.00	431.00	280.00	594.00	344.00
Total area (ha)	154291.59	154377.28	309062.99	309182.94	463830.68	463963.47	618849.15	618845.57
Mean polygon area (ha)	685.74	1050.19	1016.65	1212.48	1076.17	1657.01	1041.83	1798.97
Perimeter (km)	1606.12	1500.18	2738.37	2439.55	3735.75	2910.53	4811.21	3756.16
Mean polygon perimeter (km)	7.14	10.21	9.01	9.57	8.67	10.39	8.10	10.92
Mean perimeter-area ratio	143.00	67.61	94.39	87.15	115.22	108.56	149.03	96.90
Mean shape index	1.95	1.87	3.36	2.19	3.79	2.53	4.89	3.61
Mean cluster fractal dimension	1.21	1.20	1.24	1.21	1.25	1.22	1.26	1.24
Mean distance to the nearest neighboring polygon (km)	3.29	4.84	2.91	3.16	2.35	3.04	1.87	2.59

Table 7.7. Percentage of preferred northern side of the region and major land feature types being selected among the total grid cells that were selected for zonation maps for the 10%, 20%, 30%, and 40% targets based on biodiversity- and people-oriented approaches. See Figure 2.11 for soil type identification.

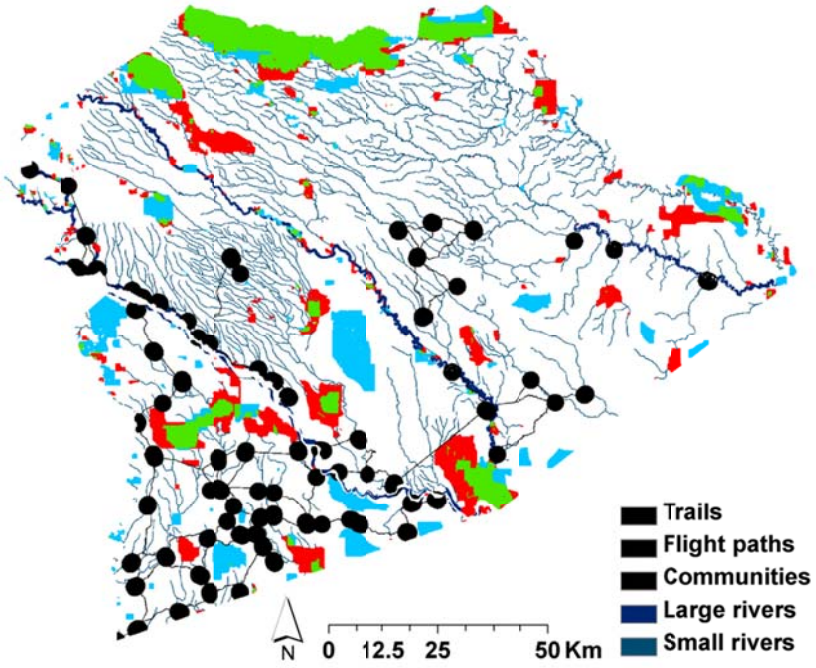
	10% target		20% target		30% target		40% target	
Land feature type	Biodiversity	People	Biodiversity	People	Biodiversity	People	Biodiversity	People
Northern side	41.64	37.48	39.27	38.58	29.33	30.07	24.98	25.14
Elevation 158-338 m	66.82	63.38	66.83	63.38	66.82	63.38	66.82	63.52
Lowland evergreen forest flat terrain	38.64	23.65	38.64	23.65	38.64	24.03	38.64	23.86
Lowland evergreen forest hilly terrain	39.65	48.52	39.65	48.74	39.65	48.53	39.65	48.53
Lowland evergreen forest white water	7.42	9.59	7.42	9.08	7.42	9.10	7.42	9.08
Palm swamp	8.70	11.83	8.70	11.83	8.70	11.83	8.70	11.83
Outside large river 200m buffer	97.30	97.30	97.30	97.30	97.30	97.30	97.30	97.30
Outside small river 100m buffer	88.91	90.88	89.03	90.88	89.36	90.88	90.44	90.88
Slope 0-12 degrees	93.47	92.87	94.64	93.89	94.77	94.34	95.08	94.66
Soil type H1	29.02	27.13	29.02	27.13	29.02	27.13	29.02	27.13
Soil type F1	9.29	8.72	9.23	10.32	9.22	9.22	9.23	8.62
Soil type F2	12.03	11.25	2.57	6.08	12.03	11.25	12.03	11.25
Inceptisol Tropept soil	12.70	13.69	12.03	11.25	13.34	12.93	13.51	13.17
Soil type K	6.62	6.19	12.69	11.86	6.62	6.19	6.62	6.19
Soil type K3	9.09	8.50	6.62	6.19	9.09	8.50	9.09	8.50
Tigre Basin	43.92	43.22	43.93	43.22	44.97	43.66	44.97	44.20
Pastaza Basin	47.59	46.84	47.60	46.84	47.60	46.84	47.60	46.84

There was a consistent approximately 50% overlap in selected areas between biodiversity- and people-oriented approaches for the 10%, 20%, 30%, and 40% targets, suggesting that these overlapping areas may be the core for a zonation map since they were selected by two different approaches. For the 10% target, the largest overlapping areas occurred on the northern side of the study region. The biodiversity-oriented approach appeared to select more small isolated patches, resulting in a less compact shape and lower connectivity (Figure 7.3A). In contrast, the people-oriented approach selected larger areas with higher spatial connectivity and lower isolation of patchiness (Figure 7.3A). The greatest overlap in selected areas occurred in the northern region where fewer indigenous communities inhabit and cultivate (Figure 7.3A). Both approaches produced solutions that included some areas with a regular and blocky shape for the 20% target (Figure 7.3B). The difference in spatial patterns and arrangement between the two approaches was even more prominent here than for the 10% targets, as the biodiversity-oriented approach selected more small isolated patches along large rivers (Figure 7.3B).

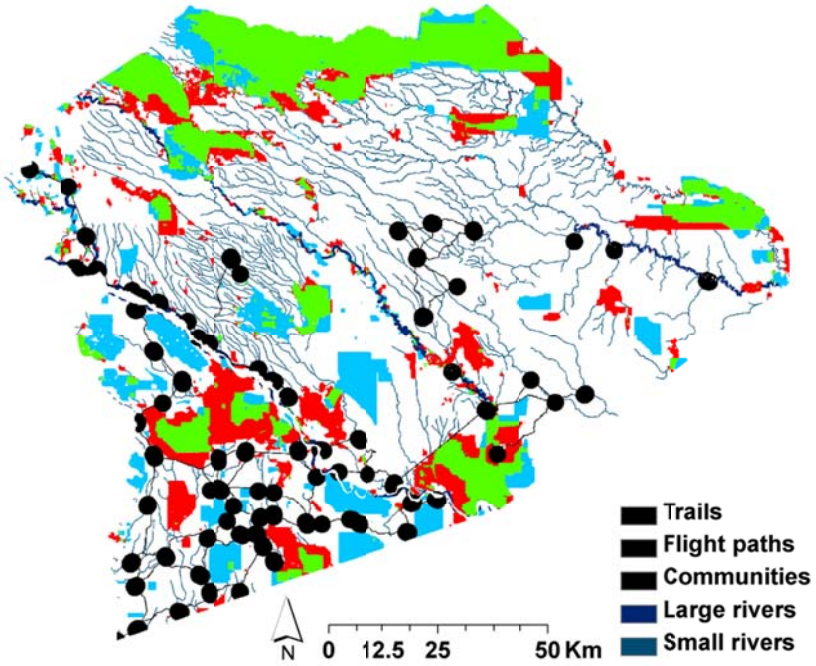
For the 30% target, the small isolated patches along large rivers that were observed from the 20% target search using the biodiversity-oriented approach had formed areas with improved spatial connectivity (Figure 7.3C). In contrast, the people-oriented approach formed a few large areas of selection with a blocky and more regular shape (Figure 7.3C). The biodiversity-oriented approach continued to show increasing spatial connectivity nearby large rivers at the 40% target, whereas the people-oriented approach retained blocky selections of large areas (Figure 7.3D). The east-central part of the study area showed the least selections for the zonation maps in both biodiversity- and people-oriented approaches (Figure 7.3D).

Figure 7.3. Sites selected by the 10% target (A), 20% target (B), 30% target (C), and 40% target (D). Red areas = sites selected by the biodiversity-oriented approach but not by the people-oriented approach, green areas = sites selected by both biodiversity- and people-oriented approaches, blue areas = sites selected by the people-oriented approach but not by the biodiversity-oriented approach.

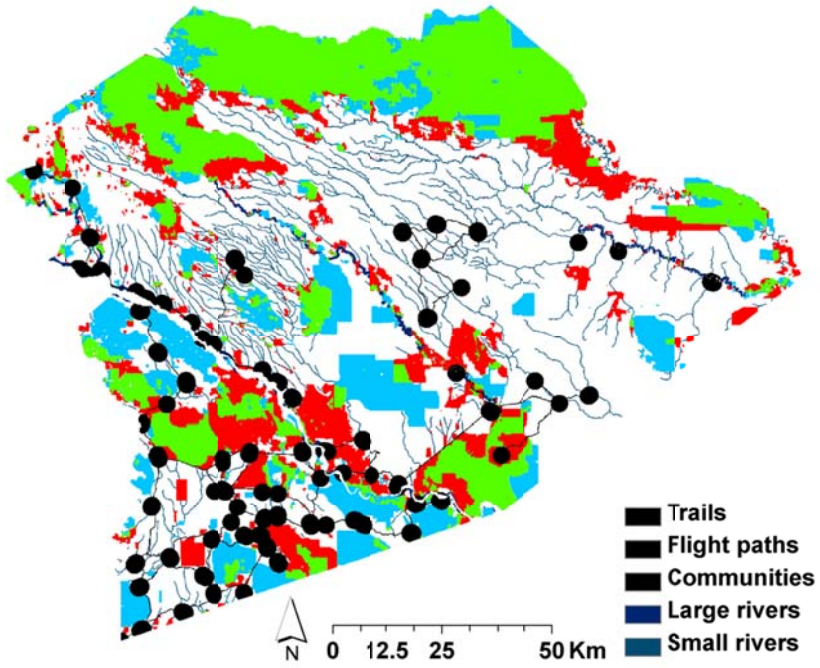
A.



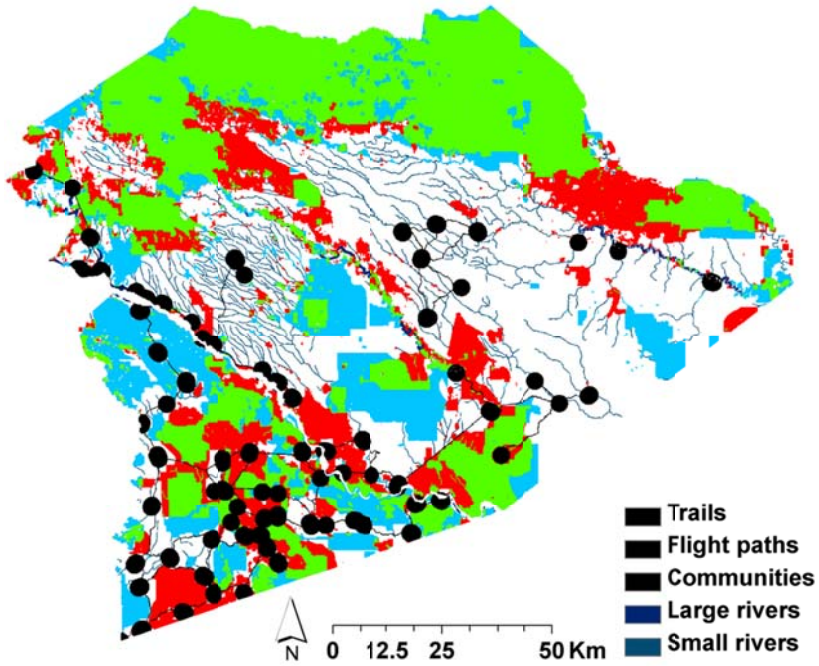
B.


Trails
Flight paths
Communities
Large rivers
Small rivers
N
0 12.5 25 50 Km

C.


Trails
Flight paths
Communities
Large rivers
Small rivers
N
0 12.5 25 50 Km

D.

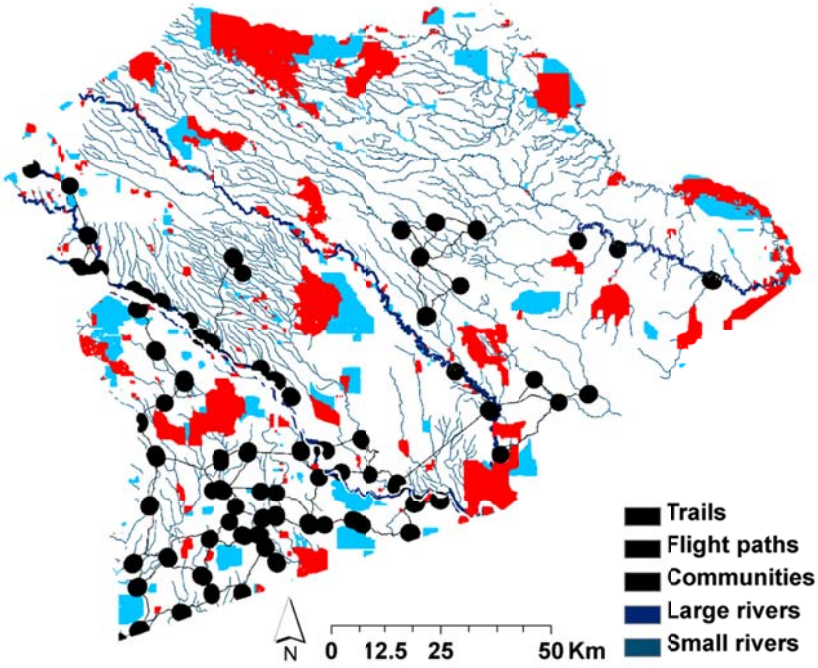


As an exercise to examine patterns of site selections under the worst-case scenario (i.e. the worst shape score according to ConsNet), initial solutions using the ILV4 heuristic algorithm (without adjacency) were constructed. ILV4 is one of ConsNet's fast heuristic algorithms that allow constructions of initial solutions to the minimum area problem (Ciarleglio et al. 2009). Similar to the best solutions described above, the solutions based on the ILV4 algorithm showed that differences in shape compactness, spatial connectivity, and site adjacency between the biodiversity- vs. people-oriented approaches were prominent for all 10%, 20%, 30%, and 40% targets. For the 10% target, there were many sporadic small patches selected by the biodiversity-oriented approach. Although with better spatial connectivity than the biodiversity-oriented approach, the large patches created by the people-oriented approach showed a blocky shape (Figure 7.4A). The poor spatial connectivity based on the biodiversity-oriented approach was

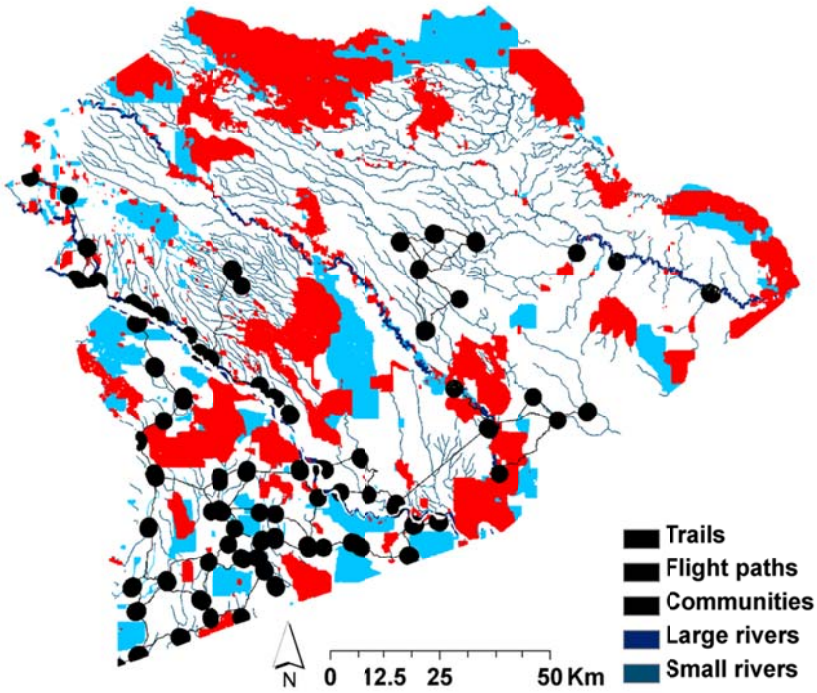
more obvious for the 20% target in which small isolated patches were distributed along large rivers. Some of the large patches selected by the people-oriented approach a showed a square-rectangular shape with blocky corners (Figure 7.4B). For the 30% and 40% targets, both approaches had blocky shapes in small and large patches, low spatial connectivity, and poor adjacency among isolated small patches (Figure 7.4 C, D).

Figure 7.4. Sites selected by the 10% target (A), 20% target (B), 30% target (C), and 40% target (D), using the ILV4 ConsNet heuristic algorithm. Red areas = sites selected by the biodiversity-oriented approach, blue areas = sites selected by the people-oriented approach.

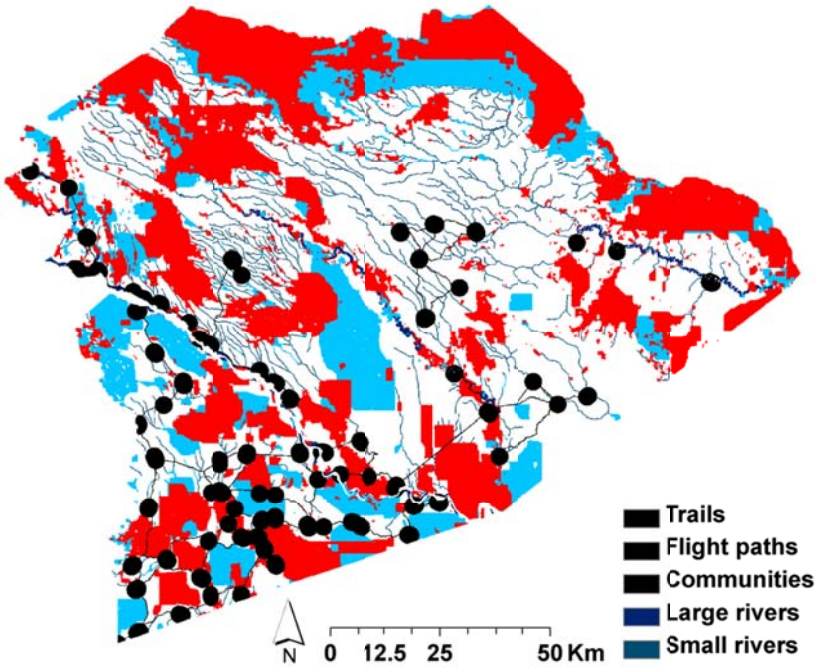
A.



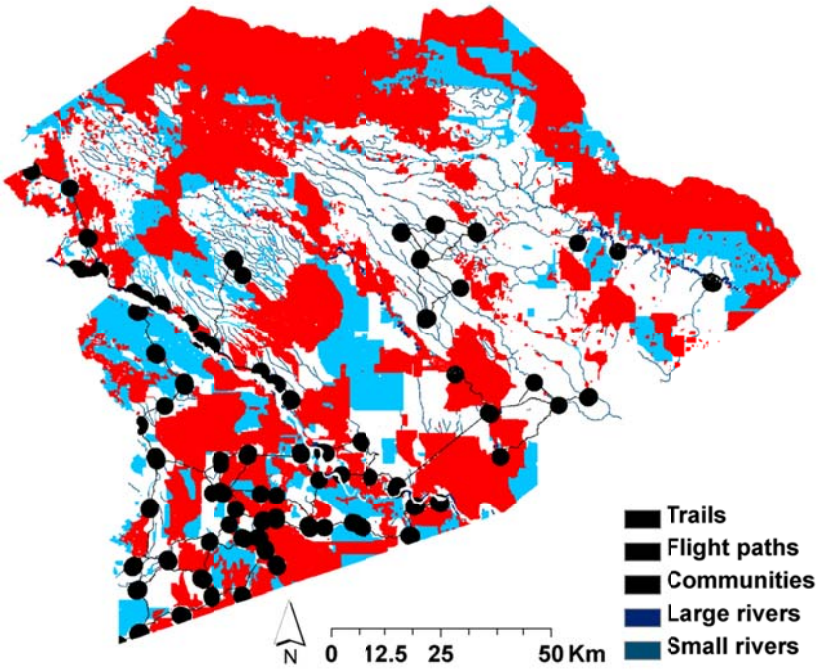
B.


Trails
Flight paths
Communities
Large rivers
Small rivers
N
0 12.5 25 50 Km

C.


Trails
Flight paths
Communities
Large rivers
Small rivers
N
0 12.5 25 50 Km

D.



DISCUSSIONS

Object-based habitat classification

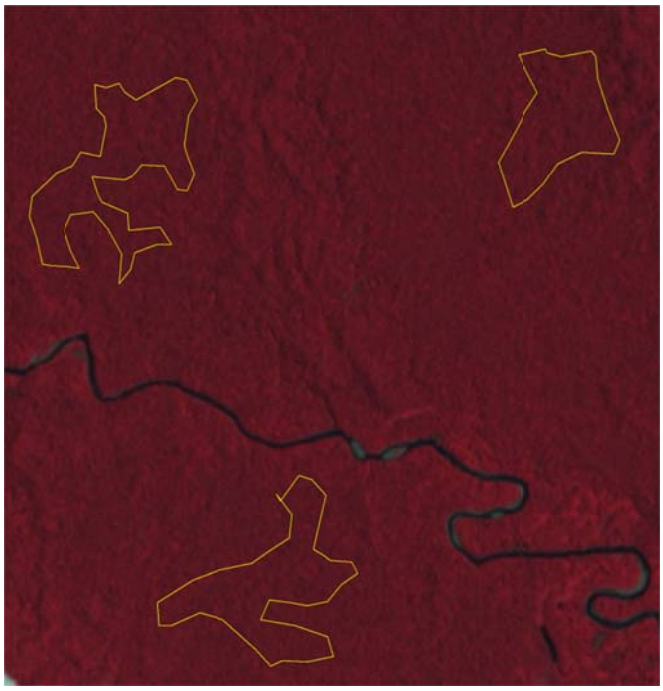
This dissertation explored the method of object-based habitat classification in order to evaluate whether or not the object-based approach provided a useful vegetation map for designing landscape zonation maps in the region. Overall accuracy of the habitat classification was nearly 80% according to both pixel- and object-based accuracy assessment methods. However, producer's and user's accuracies for individual classes varied greatly. Classifications of water and human land use achieved the highest accuracies compared to other vegetation types. Objects of water bodies, villages, and farms have low spectral, textural, chromatic, and spatial heterogeneity and therefore are easier to be extracted. The low variation within the same land cover type facilitated

feature extractability. These objects tend to be discernible, even visually, because of their aggregated distribution patterns. In contrast, extracting particular forest types for vegetation classification was a lot more challenging. Lowland evergreen forests on flat and hilly terrain contained features with similar color, texture, tone, and wide-range distributions (Figure 7.5A, B). Thus, variation within the same forest type might be relatively high, whereas the characteristics between two different forest types might be relatively similar.

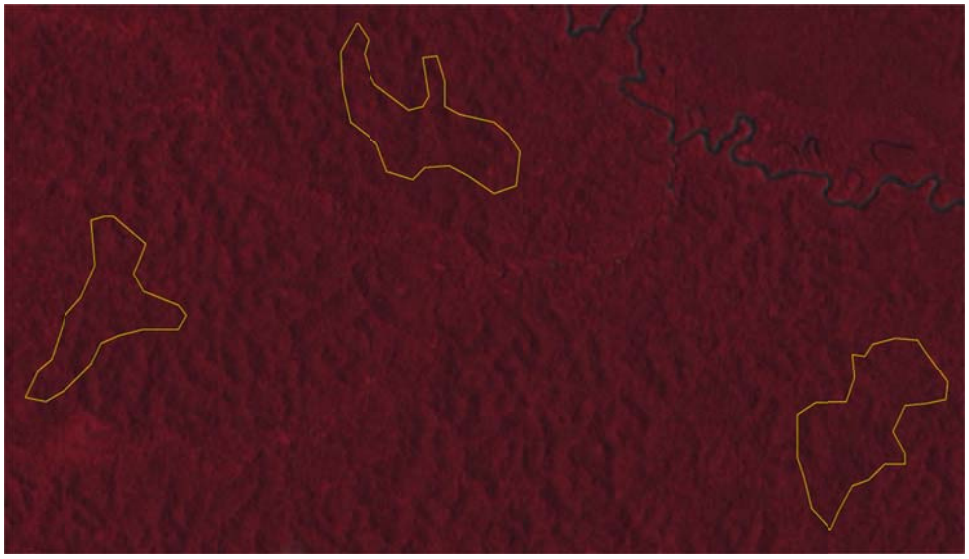
Likewise, although lowland evergreen forest in white water areas (Figure 7.5C) predominantly occurred in floodable wetlands adjacent to large rivers, great within-feature variation might enhance the challenge of distinguishing this forest type from certain features of lowland evergreen forests on flat and hilly terrain. Strong spatial association existed between lowland white water forests and rivers, which might facilitate the classification despite the within-feature variation in between lowland white water forests. Palm swamps are visually discernible with its unique texture (Figure 7.5D), albeit occasionally lowland evergreen forests on flat and hilly terrain were misclassified as palm swamps.

Figure 7.5. Examples of features (in yellow polygons) in lowland evergreen forests on flat terrain (A), hilly terrain (B), in white water areas (C), and palm swamps (D) in a pan-sharpened Landsat ETM+ image.

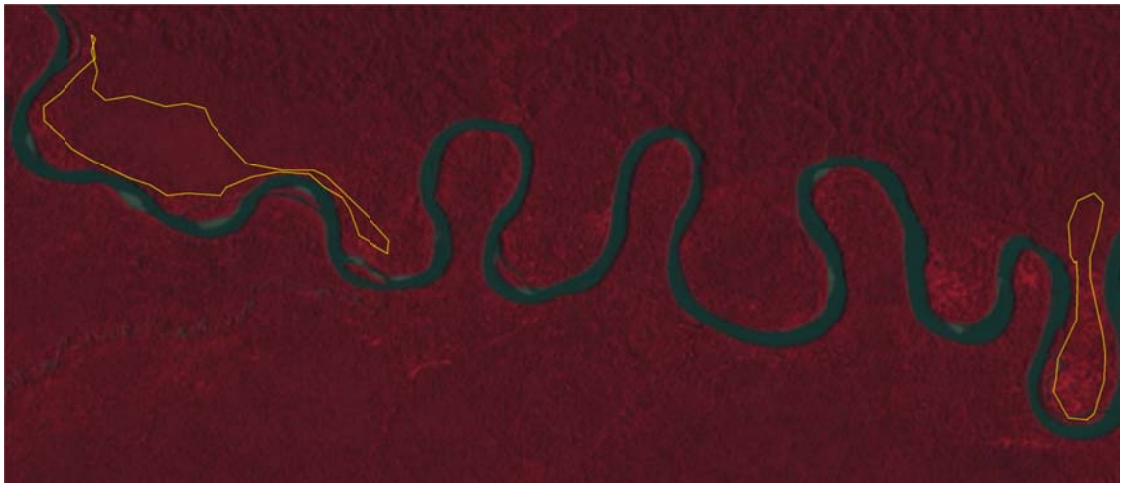
A.



B.



C.



D.

A few factors could affect the classification accuracies in this study. First, none of the four pan-sharpened Landsat ETM+ images was 100% cloud-free. Certain features of cloud and cloud shadows were misclassified as other classes. Due to the limitation in data availability and quality in the study area, these four ETM+ images were the best sources

for classification. Second, the classification scheme was based on a preliminary pixel-based unsupervised classification of ETM+ images at a 30-m resolution. An accuracy assessment of this pixel-based classification was not performed (Lopez 2008). Lopez's habitat class assignment was derived from expert knowledge and a digital elevation model (DEM) of the study area (S. Lopez, personal communication). I used features that represented habitats defined by Lopez (2008) as training examples, but potential bias might exist since I did not have sufficient ground-based data to assist in training sample delineations. Third, the distinction among certain vegetation types might not be pronounced enough. Although I was confident in determining the habitat types by visual inspections, these vegetation types might not differ prominently in spectral, textural, and chromatic aspects at the landscape scale. For example, elevation of most of the study area ranges between 150-400 m, with slope less than 20 degrees (see Chapter 2: Study Area). The lack of strong regional topographic heterogeneity might affect the differentiation between forests on flat vs. hilly terrain. Fourth, all vegetation types, except for secondary forests and shrub and herb vegetation, have nearly 100% canopy cover from a remote sensing (aerial) view. Dense, heterogeneous, and species-rich canopies make it more difficult for Landsat sensors to capture reflectance differences in substrates among vegetation types. The minor differences among substrate types in these different vegetation classes might not be captured at the classification's spatial resolution.

Studies that employed object-based image analysis (OBIA) approach have aimed to delineate tangible objects (which are made up of multiple pixels) while combining image processing and GIS functions to utilize spectral and contextual information from remotes sensing data (Blaschke 2010). OBIA allows researchers to take advantage of detailed object characteristics captured in images with fine spatial resolution, as well as images at typical Landsat (30 m) or ASTER (15 m) resolutions. In regions with more

complex land cover types, OBIA land cover mapping using Landsat or ASTER images tend to have moderate accuracies. For instance, OBIA classification of multiple categories of degraded landscape in northeastern China obtained 74% of overall accuracy (Gao 2008). A study of mapping wetlands in Canada showed 75% of overall accuracy, whereas another land cover classification study in New South Wales had 70% of overall accuracy (Gremier et al. 2008, Pringle et al. 2009). In contrast, OBIA classification can achieve high accuracies in extracting single features or in mapping more homogenous landscape in temperate regions (e.g. Matinfar et al. 2007, Johansen et al. 2008, Frohn et al. 2009, Pasher et al. 2009, Zhou and Troy 2009). Compared to these studies, the object-based classification in this dissertation was carried out in a very complex and heterogeneous landscape where the spectral and contextual variation within each vegetation type is prominent. The mosaic of land cover patches do not distribute along much bioclimatic, edaphic, or topographic gradient, making the spatial segmentation process challenging. Hence, an overall accuracy of nearly 80% is considered satisfactory and this classification is determined to be useful in providing references for future conservation planning.

The abovementioned previous studies mostly used remote sensing images from regions with less dense canopy cover, less heterogeneous canopy structure, and less diverse canopy species composition. My dissertation study is a pioneer in terms of employing object-based feature extraction techniques to classify habitat types in the Amazon at a medium spatial resolution (15 m). A few approaches may be taken in future research to improve the object-based classification accuracies. First, delineating more training examples for each class (currently n = 25) may facilitate Feature Analyst's efficiency in extracting correct features for each habitat type. Second, the object-based approach can be taken in smaller areas within the study region where remote sensing data

of higher spatial resolution is available. More still footages of very fine-resolution (5 cm) digital videos have been acquired by R. Sierra. Future object-based vegetation classification can benefit from using these high-resolution aerial photographs to facilitate creating training examples. Third, if extensive funding and project timeline are available, launching tasks to acquire fine-resolution multispectral images such as SPOT, IKONOS, or QuickBird will allow more spectrally, texturally, chromatically, and spatially distinguishable features to be extracted.

Traditionally researchers conduct Landsat-scale land cover classification in the Neotropics by using pixel-based methods. For example, Pan et al. (2004) and Kintz et al. (2006) classified land use patterns in the Ecuadorian Amazon and in the Peruvian Andes, respectively, with a hybrid (unsupervised and supervised) method. Likewise, McCleary et al. (2008) used pixel-based hybrid classification and panel analysis of trend trajectory to characterize land use and land cover change (LULCC) in the Peruvian Amazon. Walsh et al. (2008) took multiple approaches including unsupervised and object-based classifications, spectral unmixing, and pattern metrics to examine the patterns of plan invasion on the Galapagos Islands. A new trend of hybrid approach that combines pixel- and object-based classifications has been adopted by recent land cover mapping studies. Hybrid classification is more accurate than individual classifiers, as observed by Zhang et al. (2007), Gao and Mas (2008), and Crocetto and Taranito (2009). Several studies have suggested that hybrid classification can effectively improve classification accuracies in 4%-12% (Castillejo-Gonzalez 2009, Gonzalez et al. 2009) or can achieve over 90% of overall accuracy (e.g. Pasher and King 2009).

This dissertation research was limited by time and labor availability to conduct pixel-based unsupervised or supervised classification in comparison with the object-based habitat classification. Future research should include both pixel-based and hybrid

(pixel- and object-based) classifications to determine the most suitable habitat classification method for the study area. For now, the vegetation map generated from the object-based classification still provides almost 80% of overall accuracy and suffices for the needs for medium-scale vegetation mapping and zonation map design.

The classification in this dissertation aimed to create a habitat/vegetation map at a finer spatial resolution (15 m) than previous vegetation maps of the study area, with an objective that ultimately this most recent land cover/habitat map would provide references for future conservation planning work. The classified land cover types contributed to features that were used for designing landscape zonation maps. The classification scheme was inherited from a previous classification product based on a remote senser's interpretations of different habitats and definitions of different vegetation types (Lopez 2008). Therefore, the land cover categorization, derived from the remote senser's own background and knowledge, might come with bias towards interpreting the landscape. As a result of the potential bias, the land cover categories may not be directly translated into how the stakeholders and indigenous communities view the landscape and desire the land cover categorization. Consequently, the divergent opinions between the remote senser and local people regarding how the landscape should be characterized may induce certain level of disagreement, as observed by Robbins (2001) by utilizing a participatory remote sensing technique in landscape mapping.

Since the ultimate use of land cover classes is to assist in developing conservation recommendations that suit the local needs, understanding and reconciling debates between the researcher and the locals regarding how the landscape should be characterized, which land cover categories to be included, and what the definitions or interpretations of land cover types are should be incorporated into part of the conservation planning processes. In order to minimize bias and avoid conflicts between

different groups, I suggest that a bridge for merging divergent interpretations of land cover categories needs to be established. Future work should consider including pre- and post-classification workshops in order to integrate different opinions and achieve in agreement regarding land cover categorization that leads to the best application on biodiversity conservation.

Zonation map design

The ultimate goal in conservation biogeography studies is to apply knowledge of biodiversity components nested within the landscape, as well as understanding of the extent to which different types of land cover features harbor biodiversity, on a comprehensive conservation planning design that suits the local and stakeholders' needs. In this dissertation, a zonation map was created as a baseline reference for future conservation are network design. By using the aforementioned vegetation map and other remote sensing and GIS data, two approaches for designing a landscape zonation map were employed. The people-oriented approach outperformed the biodiversity-oriented approach. Shape, connectivity, size, and compactness of the selected areas under 10%-40% targets under the people-oriented approach were better than the biodiversity-oriented approach because the selections were less patchy and isolated. Furthermore, the people-oriented approach selected greater percentages of palm swamps and lowland evergreen forest on hilly terrain and in white water areas, areas that are less likely to be inhabited and cultivated by the indigenous communities (Lopez 2008, Lopez and Sierra 2010). The most profound difference between these two approaches that led to better results of a zonation map using the people-oriented approach might be the criteria regarding distances to large and small rivers. The people-oriented approach aimed to maximize distances to rivers in order to avoid conflict with local needs, whereas the biodiversity-

oriented approach sought to minimize distances to rivers in order to preserve aquatic species diversity. However, the study region consists of dense distribution of small rivers. As a result, 20% of the grid cells showed less than 4 km of distance to the nearest large river. For distance to the nearest small river, 50% of the grid cells were less than 1 km away, 80% were around or less than 2 km away, and 90% were less than 3.3 km from the closest small river.

For the biodiversity-oriented approach, selecting grid cells that are close to large rivers resulted in large clusters in a small portion of the zonation map. Choosing grid cells that are as close to small rivers as possible caused selections of a great proportion of small and fragmented areas nearby dense networks of small rivers. Maximizing distance to large rivers for the people-oriented approach did not appear to affect the zonation map since most grid cells in the study region are not close to large rivers. Because dense networks of small rivers occur in the majority of the study region, maximizing distance to small rivers increased the likelihood of selecting areas that are not fragmented by small rivers. At 10% and 20% targets, the mean distance to the nearest small river from selected grid cells was 2.7 and 2.5 times higher, respectively, for the people-oriented approach than the biodiversity-oriented approach. The difference in the mean distance between the two approaches decreased as the target increased, but at the 40% target the mean distance for the people-oriented approach was still 1.5 times greater than the biodiversity-oriented approach. Although selecting areas that are as away from rivers as possible granted more opportunities for indigenous land use, only small rivers within the vicinity to local communities are expected to be visited. Therefore, maximizing distance to the rivers that are within a particular radius of buffer zones centered by indigenous land use may be a more efficient approach. This approach is feasible for future examination because it takes into account of potential indigenous usage and does not

compromise on protecting large number of diverse taxa in the aquatic and wetland ecosystems. However, whether or not this approach suits the local needs has to be carefully examined in the future to ensure that the approach is practical and useful.

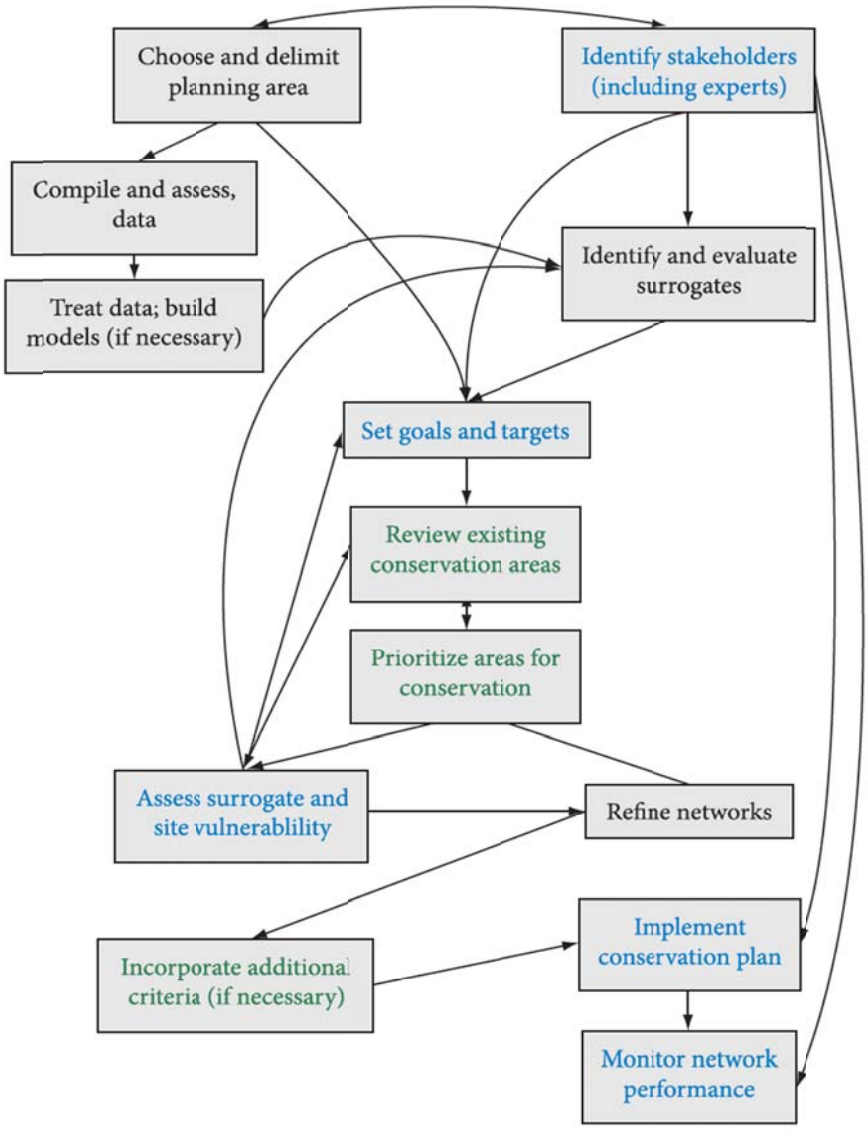
Furthermore, an integration of the selection results based on both people- and biodiversity-oriented approaches may result in a more efficient zonation map. For all targets, there was a consistent 50% overlap in selected areas between the two approaches. The overlapping areas may be the best core areas for future conservation work. Selection within the non-overlapping areas requires further examination of spatial connectivity, compactness, and alignment. For example, sites that are near large and small rivers but are away from indigenous communities should be equally preferable compared to sites that are away from rivers. Likewise, areas that are located in lowland evergreen forests on flat terrain but are outside the vicinity to community centers, hunting and walking trails, and cultivation lands should be considered as important for future conservation as sites that are in rarely-used wetlands and hilly habitats. A hybrid approach can achieve the goal of potentially protecting diverse taxa while local needs are taken into account.

This dissertation research provides preliminary zonation maps in the Ecuadorian Amazon, as an exploratory analysis that used a wide range of uniform targets. Despite the lack of any conservation and natural resource management policies in the study region, these zonation maps should only serve as a basic map based on exploratory exercises, not a final product, for the Ecuadorian Amazon. The indigenous inhabitants who know the region, culture, organizations, and the environment should be invited to participate and help with the elaboration of the regional management plan. Montoya (2010) suggested that natural resource management and conservation programs need to incorporate both environmental considerations and socio-economic, political, and cultural characteristics of a region. Due to the limitation in funding and time, I was unable to visit multiple

communities and conduct comprehensive interviews in regard to the importance of habitats from perspectives of local land use. Incorporating local considerations of habitats for land use has proven to be a strong and effective step to take during the multi-criteria analysis for a case study in Merauke, Indonesia (Sarkar et al. unpublished data). Future research should include extensive interviews in the Ecuadorian Amazon to obtain 1) local evaluation of the biodiversity-, people-, and hybrid-oriented zonation maps, 2) local opinions regarding the necessity and magnitude of land use in each habitat type, and 3) local desire in designing a conservation program that suits cultural and socio-economic needs. Based on the results of these interviews, the original zonation maps should be recreated to incorporate local concerns.

In the updated protocol of systematic conservation planning, Sarkar and Illoldi-Rangel (2010) listed a 14-component protocol (Figure 7.6). My dissertation analysis consists of part of early-stage components but the analysis could not be carried out in full alignment with the protocol due to limitation in data availability, budget and time, and the logistics. For choosing and delineating planning area, the boundary of the study region was mainly determined to include territories of multiple indigenous nationalities. For identifying all stakeholders, this dissertation research belonged to a large initiative of conservation and natural resource management plan. R. Sierra, the principal investigator of the initiative, identified stakeholders and played the role of a main bridge of communications among institutions and stakeholders. The Achuar, Shiwiar, and Zapara nationalities and communities within each nationality were the local stakeholders.

Figure 7.6. The updated protocol of systematic conservation planning (Figure 1 from Sarkar and Illoldi-Rangel 2010). Text in green indicate aspects that are well-understood, text in black are aspects which are fairly well-understood, and text in blue are aspects that remain poorly understood (Sarkar and Illoldi-Rangel 2010).



For compiling and assessing data, I began compiling GIS and remote sensing data of the study region in 2006. GIS data came from various sources of locally delineated

GIS information and regionally collected data. Remote sensing data came from archived Landsat and ASTER satellite images, SRTM, HYDROSHEDS, and WorldClim rasters, and acquired fine-resolution aerial photographs. For this dissertation analysis, only selected GIS/remote sensing data and remote sensing-based habitat classification were used due to the constraint of spatial resolution and extent of the data. In terms of treating data and constructing models, I did not construct habitat suitability models for selected species in the study region or attempt to incorporate the models into the analysis because the available species occurrence information in the region is highly localized at both ground (three 1-ha tree inventory plots) and remote sensing (aerial photographs) levels. However, the habitat classes for designing zonation maps were corrected through tedious hierarchical learning processes in feature extractions and accuracy assessment (see above) in order to achieve data refinement. I also went through series of data merging, rescaling, masking, and reclassification to treat other input data.

The protocol requires identifying and evaluating biodiversity surrogates. Due to the lack of sufficient species occurrence information, this analysis was conducted by using landscape features that did not directly represent biodiversity but rather inherited my potentially biased interpretations regarding the degree of importance of the landscape for biodiversity. A major challenge was the very limited data availability and the varying spatial resolution and accuracies of available data. The only solution is to continue updating and obtaining high-resolution data to improve data quality. Setting explicit goals and targets is required in systematic conservation planning. Ideal targets must have proper spatial configuration and ensure that adequate biodiversity protection is constituted. There is no policy, local expectations, local expertise, or prior ecological evidence to determine and support a certain threshold of representation target in this dissertation research. Therefore, in this study I conducted an exploratory analysis with

four sets of uniform targets in two approaches. The results provide a basic map to present landscape zonation under different targets, but these results do not represent conservation area networks because an adequate protocol for developing suitable targets is still in demand.

In terms of reviewing existing conservation areas for performance with respect to targets and prioritizing additional areas for conservation management, there are no existing conservation areas in the region or any conservation sites adjacent to the region. However, future research should maximize the effort of communications with stakeholders and other NGO members who work on natural resource management and sustainable development projects in the region, in order to gather the most comprehensive information to develop proper criteria and goals that take socio-economic, political, and other spatial constraints into consideration. Systematic conservation planning requires assessing vulnerabilities of biodiversity constituents and selected areas and refining the network or selected areas. Currently this study region is not facing threats from petroleum, logging, road construction, or any other large-scale development plans. However, it may still be threatened by ecological or global change factors, as well as any other anthropogenic factors.

Finally, systematic conservation planning consists of carrying out multi-criteria analysis, implementing conservation plan, and monitoring network performance. What this dissertation research can provide is the initial information to serve stakeholders and indigenous communities a map for future baseline assessment, zonation mapping refinement, multi-criteria analysis that incorporates non-ecological factors and constraints, conservation planning, and long-term monitoring.

Oil exploration and oil extraction in eastern Ecuador began in the 1940s, were temporarily abandoned in the 1950s, and resumed in the 1970s in areas newly vacated by

the relocated Waorani indigenous group (Finer et al. 2009). Yasuní National Park was created in 1979 and has been exposed to road construction, oil development, and illegal logging (Finer et al. 2009) (Figure 2.1). In 2007 the "Zona Intangible" was delineated to set areas off-limits to extraction activities. Ecuador then launched an innovative Yasuní-ITT initiative to propose perpetually leaving oil locked beneath the ground to protect biodiversity, indigenous people, and to battle climate change (Finer et al. 2010). A large amphibian, bird, mammal, and plant distribution synthesis indicated that eastern Ecuador and northern Peru are the only regions in South America where species richness centers for all four taxonomic groups overlap (Bass et al. 2010). The study by Bass et al. provided scientific recommendations and conservation significance of Yasuní National Park, suggested that new oil activities and road construction need to be stopped, and recommended stakeholders to create areas off-limits to large scale development (Bass et al. 2010). Being one of most biodiverse regions on Earth, Yasuní National Park in northeastern Ecuador is the only viable strictly protected area in eastern Ecuador and is yet facing threat from oil development that jeopardizes Yasuní's conservation values (Bass et al. 2010). Such under-representation of conservation effort in Ecuador has been mentioned by Sierra (2002), who pointed out that although 14% of the terrestrial lands in Ecuador fall within protected areas, some habitats are underrepresented. Likewise, Thomassen et al. (2011) used reserve selection algorithms to prioritize conservation areas in Ecuador based on intraspecific variation and found that priority areas mainly occur along Andean slopes but are not well represented in existing reserves. The study area in my dissertation is a typical case of under-representation in Ecuador: located in a highly biodiverse region where no viable systematic conservation planning program has been implemented. My dissertation draws a preliminary sketch of landscape zonation, but

subsequent steps as discussed above must take place in response to the pressing needs for an implemented conservation program in order to fill in gaps in eastern Ecuador.

Sarkar et al. (2009) identified six limitations in a systematic conservation assessment in Mesoamerica, Chocó, and tropical Andes. These limitations may be common challenges that systematic conservation planning faces in other regions: 1) Species distribution models only model a small percentage of species on the IUCN Red List and a lot of these species are from particular taxa. 2) Only species that are considered at risk by IUCN are used in conservation assessment, but there should be integration with a subregional (e.g. national) conservation priority list of species at risk. 3) The resolution of land cover dataset may be too coarse to capture anthropogenically transformed areas. 4) Classification of the entire study region into ecoregions may be too coarse and regional classifications at finer resolution are missing. 5) Spatial criteria, such as spatial connectivity, shape, dispersion, and alignment should be incorporated into the conservation area network design. 6) Stakeholders need to be brought in as decision makers and information providers regarding socio-political constraints or opportunities. A few approaches may facilitate in improving the effectiveness and efficiency of conservation planning. For example, targets of representation can be based on current conservation status of the target species in order to make better ecological senses of the targets (Illoldi-Rangel et al. 2008). Moritz (2002) proposed a strategy to identify areas that are important to represent species and genetic diversity, and then maximize the protection of environmental gradients within these areas in order to maintain population viability and genetic diversity. In addition, using genetic and morphological traits of common species as surrogates for endangered species can effectively catalyze collaborative efforts among conservation biologists (Fuller et al. unpublished data). Although in 2008 the new Ecuador Constitution banned oil extraction in protected areas

(Finer et al. 2010), my study region in southeastern Ecuador may still face potential large-scale development if a conservation planning program is not launched soon in order to determine potential conservation sites and strategize conservation plans.

Chapter 8: Conclusions

Conservation biogeography is an applied discipline that entails biogeographic theories and analyses concerning the distribution and the conservation of biodiversity (Whittaker 2005). Understanding species diversity patterns must take place as an initial step to facilitate approaching the application of conservation biogeography. To understand species diversity patterns in southeastern Ecuador, in this dissertation I used tree inventory plots to examine some of the widely discussed mechanisms in explaining tree diversity. Because processes that regulate diversity gradients appear in a spatial hierarchy from local to the landscape level (Hill and Hill 2001), this dissertation research first characterized alpha diversity patterns in southeastern Ecuador and then extended the study into beta diversity characterization in western Amazonia.

ALPHA DIVERSITY AND FOREST STRUCTURE IN THREE 1-HA PLOTS IN SOUTHEASTERN ECUADOR

For this dissertation research, my collaborators and I established the first permanent 1-ha tree inventory plots in southeastern Ecuador. Temporary transects were laid out for rapid tree inventories in southeastern Ecuador (EcoCiencia and M. Tirado, personal communications), but my dissertation research was the first that obtained community approvals for permanent tree plots in which all trees ≥ 10 cm DBH were tagged, documented, and identified. Periodic (i.e. every five years) recensuses of these 1-ha plots will allow the first long-term forest dynamics and monitoring study in southeastern Ecuador. Unfortunately access to the Yutsuntsa plot was denied in 2008, but a revisit is hopeful in the future with greater efforts in communication and negotiation with the Yutsuntsa community.

Furthermore, this study fills in gaps of tree inventories in southeastern Ecuador within the network of Neotropical (especially Amazonian) rainforest plots. Eastern

Ecuador has been identified as a hotspot of species richness and one of the most biodiverse regions on earth (Bass et al. 2010), but tree inventory data in southeastern Ecuador has not been available for integrated regional diversity studies. My plot data will become part of the RAINFOR database, The Amazon Forest Inventory Network (http://www.geog.leeds.ac.uk/projects/rainfor/), Forest Plots Database, a database for continental forest inventories (http://www.forestplots.net/), SALVIAS, a Latin America-biased plant database (http://www.salvias.net), as well as the Amazon Tree Diversity Network (ATDN) (http://web.science.uu.nl/Amazon/ATDN/). My plot data (partially shown in Appendix C) will complement current data in northeastern Ecuador and provide valuable information for examining regional, continental, or even global diversity patterns.

A combination of microhabitat variation and geographic distance may both contribute to the high number of species and great place-to-place differences. The hypothesis that species distribute along a gradient of heterogeneous canopy opening, soil properties, or topography is not supported. At the within-plot level, no obvious species assemblages according to the ordination analysis or high correlations between ordination axes and environmental variables were found within the plots in Yutsuntsa, Juyuintsa, and Sawastian. These results implied that neutral processes, such as stochastic events or dispersal limitation, may contribute to the floristic variation in species composition (Hubbell et al. 1999, Hubbell 2001). Within-plot floristic variation may support neutrality, which argues that species diversity rises at random, as each species follows a random walk (McGill 2003). However, niche differentiation resulting from interspecific competition that is not examined here, may also play a role in alpha diversity patterns. In contrast, strong species assemblages at the plot level corresponded to the relative geographic locations of Yutsuntsa, Juyuintsa, and Sawastian. Such strong assemblages in

species composition occur among plots and indicate that geographic distance or regional dispersal limitation may play a more important role influencing diversity patterns at a broader scale.

This dissertation aimed to examine if size class and height of trees within the three 1-ha inventory plots show random or clustered distribution, as well as the extent to which within- and between-plot variation in species diversity and distribution is affected by the biophysical environment. The hypothesis that spatial heterogeneity in size class and height is not randomly distributed is supported. I found spatial clustering at particular distance ranges, as well as dispersion (i.e. repulsion) and attraction (i.e. clustering) observed at different distance ranges between individuals of canopy vs. canopy, canopy vs. subcanopy, and subcanopy vs. subcanopy trees. A future closer examination on the spatial relationships between understory and subcanopy/canopy trees may shed light on tree point patterns that may be influenced by mortality and recruitment, thus giving insights into population dynamics. In addition, neighborhood associations between dominant trees in different families, genera, and species may be important in influencing spatial distributions. A future examination of the spatial relationships between dominant species/genera in different size or height classes may shed light on ecological interactions, such as interspecific competition or non-competitive coexistence (e.g. Condit et al. 2000). Besides further examining spatial interactions between dominant taxa, I argue that scale dependence in spatial point pattern and neighborhood analysis may affect how spatial clustering vs. dispersion and attraction vs. repulsion is defined. The changing point patterns in different neighborhood sizes in this dissertation study indicated the complexity of examining tree distribution and how "scale" of examination (e.g. the neighborhood size) may affect the interpretation of the local tree distribution. Studying "multiple scales of clustering" of spatial patterns at a particular distance or a

spatial point at multiple distances should be the goal of future research (Wiegand et al. 2007c).

Although one of the three 1-ha plots harbored a greater percentage of successional species than the other two plots and therefore might have experienced relatively recent disturbances, these three plots are among the most biodiverse tree plots on Earth compared to other inventories in Latin America and Asia (e.g. Condit et al. 2004, Lee et al. 2004, Leigh et al. 2004). These plots have great within- and between-plot species dissimilarity, partially contributed by the very high percentage of species (approximately 50%) with only one individual in the plot. The lack of a distinctive dry season in southeastern Ecuador may provide suitable bioclimatic environment for species coexistence. This dissertation depicts the floristic patterns of tree diversity in southeastern Ecuador at local (within-plot) and regional (between-plot) scales and demonstrates the uniqueness of the forests and hence their importance in conservation.

BETA DIVERSITY AMONG ONE-HA PLOTS IN EASTERN ECUADOR AND NORTHERN PERU

This dissertation research also provides information for future beta diversity studies that will include the tree plot data from southeastern Ecuador. By joining the abovementioned forest plot networks, this dissertation data fills in gaps of tree diversity studies in southeastern Ecuador. Plots in northeastern Ecuador have been used for large-scale tree diversity studies (e.g. Pitman et al. 2001, Pitman et al. 2008), but this dissertation is the first that incorporates data in southeastern Ecuador into a comparative study for one of the world's biodiverse hotspots. By stretching available tree plot data from northeastern into southeastern Ecuador, a better understanding of tree beta diversity patterns and biogeography is achieved.

The three 1-ha plots that I established in southeastern Ecuador harbored greater percentages of both common (≥ 1 individual/ha) and extremely rare (singleton) species, as well as species that were shared by plots in Ecuador and Peru compared to plots in northeastern Ecuador and Peru. More than 35% of species in southeastern Ecuador is common or extremely rare species, suggesting the coexistence of potential habitat specialists and generalists and opportunities for some rare species to establish and persist. The plots in southeastern Ecuador have a higher percentage of species shared by Ecuadorian and Peruvian plots, suggesting the biogeographic importance of the flora in this region. More than half (> 60%) of individual trees in the Ecuadorian and Peruvian forests were dominated by "oligarchy", i.e. a small set of common species of high local abundance (Pitman et al. 2001). More specifically, the oligarchy in southeastern Ecuador rose from a small number of species with higher landscape-scale density than the oligarchies in northeastern Ecuador and Peru. The more pronounced oligarchy in southeastern Ecuador may contribute to the lower species diversity compared to plots in northeastern Ecuador and Peru.

The western and eastern forests in this dissertation study showed changes in landscape-scale density of common species, shift in species composition, and discontinuity of tree species (Pitman et al. 2008). Percentage of shared species decreased from the direction of southeastern to northeastern Ecuador and to northern Peru, suggesting that the three 1-ha plots in southeastern Ecuador may be in a unique biogeographic region that harbors certain favorable edaphic, topographic, or hydrological conditions to allow a great number of species to establish.

The dissertation studies support the hypotheses that 1) differences in tree species diversity and distribution among tree plots increase with their geographic distances and 2) the bioclimatic differences among the plots also account for the beta diversity. The

resulting discontinuity in species composition and change in oligarchy may be the main factors that influence beta diversity in Ecuador and northern Peru. Climatic variability driven by seasonal variation particularly in quantity and distribution of precipitation was correlated to species diversity in a broader spatial scale (ter Steege et al. 2006, Stropp et al. 2009). How seasonality plays a role in governing beta diversity, especially how rainfall seasonality regulates tree diversity patterns by affecting species shade tolerance and functional type should be examined in the future (ter Steege et al. 2003).

The species oligarchy and shifts in oligarchy, as well as the significant relationship between variation in floristic composition and geographic distances between paired plots, implied dispersal limitation or regional differentiation/replacement of at least dominant species. The dissertation study results indicated that dispersal limitation and precipitation seasonality are potentially the most important factors that contribute to tree beta diversity in western Amazon. Competition among species is not examined in this dissertation, but this mechanism can potentially result in coarse-scale niche partitioning.

This dissertation complements a sketch of the unique eastern Ecuador-northern Peru species diversity patterns. It examines beta diversity patterns and finds congruence with a few important beta diversity studies in the Amazon (see above). The species richness center in eastern Ecuador-northern Peru is now facing threats from petroleum development, logging, road construction, and other anthropogenic transformation (Bass et al. 2010, Finer et al. 2009, Finer et al. 2010). Although southeastern Ecuador currently harbors great biodiversity and has minimal anthropogenic disturbances, linking diversity information to the rest of biodiverse hotpots will facilitate in understanding of factors and mechanisms that contribute to large-scale diversity and in making recommendations of strategic conservation planning for preserving biodiversity.

REMOTE SENSING-BASED CANOPY SHADOW AND PALM DISTRIBUTION IN SOUTHEASTERN ECUADOR

Biogeographers have been using remotely sensed data and methods for characterizing tropical forest canopies, as a more efficient approach to address the major challenge in lack of tropical forest data in remote areas and an unbalanced sampling effort between remote areas vs. areas with easy access (Turner et al. 2003, Cayuela et al. 2006, Saatchi et al. 2008).

As the first study that successfully extracted forest canopy shadows from very high resolution aerial photographs using object-based classification techniques, my dissertation research offers a set of repeatable and semi-automated methods that can be applied on other studies in which features with distinctive colors and texture need to be extracted from non-multispectral remote sensing imagery. For instance, the methods of image preprocessing and hierarchical learning can become templates for feature extractions of particular tree crowns with discernible phenological traits, tree trunks with unique architecture (e.g. baobab trees in Africa, K. A. Crews, personal communication), or canopies with distinct structure (e.g. palms). Researchers who have access to fine-resolution non-multispectral images will be able to take advantage of object-based feature extraction techniques as an alternative of the pixel-based classification approach.

All three accuracy assessment methods used for evaluating the object-based extraction of canopy shadows from aerial photographs indicated high accuracies and success of feature extraction techniques for non-multispectral remote sensing data. The classification showed over 90% overall accuracies using object- and pixel-based assessment approaches, and over 80% of extracted features are in areas with over 50% cover of real canopy shadows. This dissertation study did not rely on any ancillary data to build an interpretation key for accuracy assessment, but still gained satisfactory results.

This approach yielded high classification accuracies that not only supported the object-based classification, but also proved the objectivity of the accuracy assessment methods. Therefore, this study also demonstrated a novel approach of efficient accuracy assessment by using the same imagery as classification input and accuracy assessment reference data. This approach proves that despite limits in data availability and spectral information, object-based feature extraction is an effective and a flexible method that retains high classification accuracies.

My dissertation research was unable to automate tree species identification from aerial photographs due to data and technical limitations, but I argue that with a combination of ground data and fine-resolution images (multispectral or preferably hyperspectral), object-oriented tropical tree identification can be feasible in a future study. The respective spectral information of certain species groups based on results of object-oriented classifications may provide information regarding density and species richness. Derivatives of spatial variation in vegetation indices, tree density, number of species, and diversity estimates of emergent and canopy trees detected in remote sensing imagery should reflect the spatial heterogeneity of local vegetation and habitat types.

The three 1-ha tree inventory plots in southeastern Amazon provided valuable floristic descriptions in southeastern Ecuador, but large-scale ground inventories are not feasible in this region due to difficulty in accessibility. In this dissertation, I identified dominate palms from aerial photographs as an exploratory analysis in order to access the feasibility of using high-resolution aerial photographs to conduct rapid inventories of canopy trees that are identifiable and discernible. The results suggested that characterization of palm diversity, distribution, and spatial associations with other palms based on aerial photographs complemented ground data in large and remote areas. An exploratory analysis that examined the association between the products of two analyses

(canopy shadows and palms) showed that density of palms was affected by size and clustering of canopy shadows, suggesting that palms appear to be indicative of some aspects of forest dynamics in their various responses to canopy gap formation. Future remote sensing research should aim to complement other palm studies that examined how palms response to canopy gaps or general disturbances (e.g. Martinez-Ramos et al. 1988, Pintaud 2006, Baez and Balslev 2007). This extended future study should first aim to extract palms in an automated way, and then elucidate whether or not density, crown size, and distribution of palms are associated with canopy gaps, in order to facilitate in understanding forest dynamics: areas with small palm canopies and larger canopy gaps may have experienced more recent stochastic events whereas areas with large palm canopies and smaller canopy gaps may show less effect of disturbances.

ZONATION MAP DESIGN IN SOUTHEASTERN ECUADOR

The habitat classification map created in my dissertation research has by far the finest spatial resolution (15 m) among currently available vegetation maps in the study region. By sharing this habitat map, I expect to offer good reference data with accuracy assessment information to stakeholders and collaborators for broader application and planning purposes. Future research needs to take into account the divergent interpretations and definitions of land cover categories imposed by different groups in order to minimize potential disagreement and bias introduced by using remote sensing data (Robbins 2001). This object-based classification map is also apparently the first that applied object-oriented land cover classification on designing landscape zonation maps. Maps of land use and land cover/change (LULCC), ecoregions, or protected areas constitute essential information for the multi-criteria analysis in conservation planning.

My dissertation research demonstrated an alternative approach to characterize the landscape and integrate the information of landscape characteristics into designing zonation maps.

This dissertation research initiated the first technical---even though preliminary---effort in creating landscape zonation maps in southeastern Ecuador by using climatic, topographic, hydrological, remote sensing, and environmental data to design exploratory maps that provided baseline information for future conservation planning. There have been demands for a multi-disciplinary program that integrates biodiversity conservation, natural resource management, and sustainable development in southeastern Ecuador (R. Sierra, unpublished data), but tangible delineation of conservation-focused areas has not been produced and presented to the local inhabitants. This dissertation presented preliminary zonation maps that aimed to balance between biodiversity conservation and local land use. The results were summarized in easy-to-understand maps for local managers (e.g. the presidents of indigenous territories and leaders of communities) to visualize and evaluate in the future. The zonation maps carried certain degree of bias inherited from multiple designing preferences and criteria based on my field observations and interpretations. By incorporating feedback from landowners and managers, these zonation maps can be redesigned with improved input criteria to take into account the stakeholders' needs and other socio-economic factors. Ultimately, a conservation area network design in this region should develop strategies for minimizing conflicts between anthropogenic development and biodiversity conservation as well as for reducing the impact of habitat degradation (Bassett and Zimmerer 2003).

More specifically, the zonation maps in this dissertation compared a people-oriented approach that selected areas less visited for indigenous land use vs. a biodiversity-oriented approach that chose areas which may harbor greater species

diversity. The people-oriented approach outperformed the biodiversity-oriented approach in the resulting shape, connectivity, size, and compactness of the selected conservation areas. Furthermore, the people-oriented approach selected greater percentages of habitats that are less likely to be inhabited and cultivated by the indigenous communities. Since both approaches consistently overlap in 50% of selected areas for zonation maps under all targets, a post-selection refinement in the future should first prioritize areas within the overlapping regions, and then take a hybrid approach to integrate selections from both approaches in order to attain balance between biodiversity conservation and needs for local land use.

Implementing a conservation planning program in the future will rely on the preliminary data and analysis generated from this dissertation. Subsequent planning steps should include workshops to conduct comprehensive evaluation of the current (preliminary) zonation maps, detailed interviews of local needs of land use in different habitats, and assessment of stakeholders' needs as well as socio-economic or political constraints. Currently more than 96% of total cultivation is dedicated to non-commercial production in the Achuar and Shiwiar territories (Lopez 2008). However, the potential overall scarcity of land resources for food production discovered by Lopez and Sierra (2010) indicated the importance of incorporating local needs into conservation planning. A future study should comprise extensive interviews to obtain knowledge of 1) local evaluation of the zonation maps, 2) local opinions regarding the land use in each habitat type, and 3) local needs in cultural and socio-economic aspects. Under-representation of conservation effort has been observed in previous conservation planning and reserve selection studies of Ecuador, especially in eastern Ecuador where Yasuní National Park is the only viable strict protection area (Sierra, 2002, Bass et al. 2010, Thomassen et al.

2011). There is still pressing need for a strategic conservation program in eastern Ecuador in response to potential large-scale development.

FINAL THOUGHTS

This dissertation highlights the two fundamental elements of conservation biogeography: understanding biodiversity patterns and applying that understanding towards conservation (Whittaker 2005, Richardson and Whittaker 2010). To this day, difficulties of integrating tree diversity mechanisms into a species diversity study still exist conceptually, practically, statistically, and analytically. Key issues for guiding future biodiversity research should include refining methods to obtain measures of alpha and beta diversity and interpreting mechanisms that influence diversity patterns (Sax and Whittaker 2004). Remote sensing techniques can be used for characterizing biodiversity features at both fine (local) and coarse (regional) scales. The challenge is the uncertainty of using remote sensing data to detect tree diversity patterns. The reliability of using remote sensing-derived measures or species diversity estimates as a proxy of biodiversity components also needs to be examined. Using remote sensing products of biodiversity features and land heterogeneity information can expand the array of knowledge used in conservation and management (Ferrier 2002, Wiens et al. 2009). However, remote sensing-based landscape characterization must be interpreted carefully to integrate perspectives from different groups (Robbins 2001). Therefore, implementing biodiversity conservation with the considerations of socio-economic costs, needs for sustainable development, and political aids remains a top priority.

My dissertation examined diversity patterns from alpha to beta diversity and from local to regional scales. Alpha diversity patterns did not appear to be associated with the biophysical environment, but whether or not the patterns were truly driven by neutral

processes (Hubbell 2001) needs further assessment. Spatial distributions and associations of alpha diversity components revealed heterogeneous and complex patterns that might be related to forest dynamics and intra- or interspecific relationships (Franklin and Santos 2011). Further examination of these spatial patterns may shed light on a question that this dissertation could not answer: does niche differentiation driven by interspecific competition contribute to alpha diversity (Connell 1983)? Differing from alpha diversity, beta diversity patterns showed associations with abiotic (bioclimatic factors) and biotic (dispersal limitation) mechanisms. The findings were congruent with other Amazonian studies of regional tree diversity (ter Steege et al. 2006, Pitman et al. 2008). Mechanisms that this dissertation data could not address include regional-scale niche partitioning driven by competition and the extent to which edaphic characteristics influence beta diversity (Tuomisto et al. 2003b). Variations in species composition and spatial distribution detected patterns that were discernible at the level of alpha but not at the beta diversity leave and vice versa. This indicated the importance and necessity of examining species diversity with an integrated approach to embrace multiple scales.

Alpha and beta diversity studies based on field research face challenges when site accessibility is limited. Remote sensing data and techniques used in this dissertation demonstrated the feasibility of characterizing alpha diversity features (canopy shadows in two indigenous communities) and beta diversity components (canopy palms in southeastern Ecuador) at a micro scale in terms of both spatial resolution and spatial extent of the data (Odum 1994). My dissertation showed that using remote sensing resources complements ground-based alpha and beta diversity studies and provides information that rapid field inventories may not be able to obtain. I propose that the micro and fine scale canopy shadow and palm distribution patterns may assist in developing proxies to indicate forest gap dynamics or disturbance history, as well as estimators of

alpha and beta diversity. In addition, micro-scale remote sensing data can be used to provide species occurrence information (e.g. palms) or forest structural patterns (e.g. canopy gaps) for constructing habitat suitability models that are used as biodiversity surrogates for systematic conservation planning (Phillips et al. 2006, Margules and Sarkar 2007).

Moving from micro to macro scales and from biodiversity proxies to conservation planning, macro-scale remote sensing information such as topography or land cover categories can facilitate conservation planning by providing environmental data for habitat suitability models and by serving as environmental surrogates for systematic conservation planning (Ferrier 2002, Margules and Sarkar 2007). Therefore, remote sensing can help bridge between field-based alpha and beta biodiversity components and coarse-scale landscape characteristics components. The bridging effort is expected to facilitate conservation because systematic conservation planning can utilize remote sensing-derived information in multiple scales for mapping biodiversity surrogates and for creating conservation area networks.

Systematic conservation planning aims to maintain biodiversity representation and persistence by addressing rarity and complementarity that are also essential components of beta diversity (Margules and Pressey 2000, Margules and Sarkar 2007). Due to the lack of sufficient regional biota information for designing conservation area networks, in this dissertation I designed landscape zonation maps by including macro-scale habitat classification using remotely sensed information as well as other remote sensing and GIS data. Due to the limitation in time, labor, and funding, the land cover classification was based on a previous classification scheme without pre- and post-classification consultation with the indigenous communities. The land cover categories used for future classification need to incorporate local interpretations of landscape

characteristics in order to create maps that recognize and compromise divergent interpretations and definitions of land cover types. Prior to applying results of land cover classification on meaningful and practical conservation work, a land cover map that incorporates diverse opinions regarding "habitats" and "land use" needs to be created to underpin the foundation of conservation planning. Furthermore, a conservation area network design requires weighing the importance of habitats from both biodiversity (biota data driven) and human (local needs driven) perspectives. Hence, the zonation maps produced in this dissertation should be recreated in the future after including local needs and perspectives on how indigenous people value the landscape and habitats in order to ensure that conservation planning does not create conflicts with local interests (Montoya 2010). The ultimate goal of conservation biogeography under the framework of systematic conservation planning should address concerns from the human dimension of the environment, especially within the complexity and constantly changing political constraints in the indigenous territories, before conservation planning efforts can be initiated.

Appendix A

List of top 30 species with the highest importance values in the three 1-ha plots.

Species	Relative density (%)	Relative dominance (%)	Importance Value
Sawastian			
Matisia lasiocalyx	17.09	4.48	21.57
Urera sp.	5.76	2.22	7.97
Guarea kunthiana A. Juss.	0.90	6.65	7.55
Guarea macrophylla Vahl.	3.24	2.80	6.04
Ficus ypsilophlebia Dugand	0.18	5.33	5.51
Pachira punga-schunkei Fer. Alonso	2.16	3.16	5.32
Acacia glomerosa Bentham	1.08	3.56	4.64
*Terminalia oblonga (*R. & P.) Steudel	1.26	3.36	4.62
Trichilia pittieri DC.	2.70	1.36	4.06
Cabralea canjerana (Vahll.) Mart.	0.18	3.74	3.92
*Pterocarpus amazonum (*C.Martius ex Bentham) Anshoff	1.62	2.14	3.76
Tachigali paraensis (Huber) Barneby	2.70	0.94	3.63
Ficus gomelleira Kunth & Bouché	0.18	3.41	3.59
Chimarris glabriflora Ducke	1.80	1.65	3.44
Sapium marmieri Huber	1.26	2.13	3.39
Phytelephas sp.	2.16	0.85	3.00
Jacaratia digitata (Poepp. & Endl.) Solms	0.72	2.23	2.95
Sloanea grandiflora Sm.	0.54	2.38	2.92
Caryodendron orinocense H. Karst.	0.18	2.61	2.79
Unknown	1.08	1.64	2.72
Sorocea steinbachii C.C. Berg	0.54	2.15	2.69
Inga auristellae Harms	1.44	1.21	2.65
Erythrina amazonica Krukoff	0.18	2.46	2.64

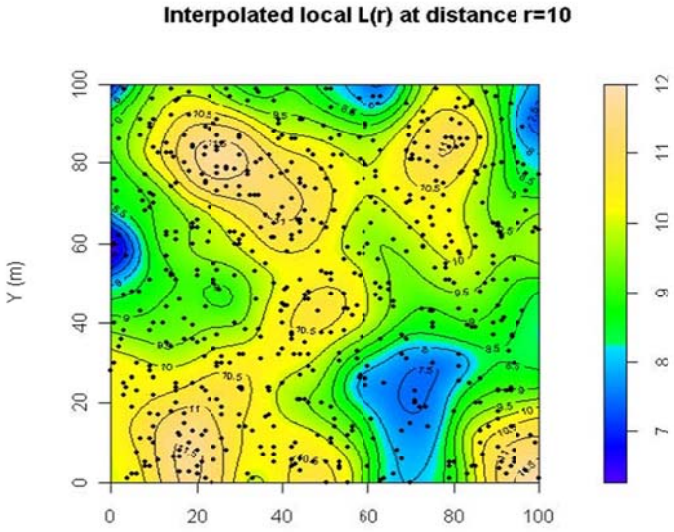
Iriartea deltoidea Ruiz & pavón	1.62	0.97	2.59
Trichilia martiana C. DC.	0.72	1.86	2.58
Kuyua	0.72	1.76	2.48
Sterculia colombiana Sprague	1.62	0.79	2.41
Trichilia septentrionalis C.DC.	1.62	0.73	2.35
Dialium guianense (Aublet) Sandwith	0.72	1.57	2.29
Inga sp. 5	1.08	1.09	2.17
Yutsuntsa			
*Iryanthera macrophylla (*Benth.) Warb.	3.9	8.7	12.6
Eschweilera coriacea (DC.) S.A: Mori	6.8	5.5	12.4
*Oenocarpus bataua (*Mart.) Burret	4.6	5.2	9.8
*Micropholis egensis (*A. DC.) Pierre	2.1	3.9	6.0
Virola flexuosa A.C. Sm.	2.4	1.0	3.5
Endlicheria aff. formosa A.C. Smith	0.5	2.6	3.1
Hevea guianensis Aublet	1.3	1.6	3.0
Virola pavonis (A.DC.) A.C. Sm.	1.5	1.4	2.9
Iriartea deltoidea Ruiz & Pavón	1.8	1.0	2.8
Pouteria sp. 1	1.6	0.9	2.5
Gustavia hexapetala (Aubl.) Sm.	0.7	1.8	2.5
Vochysia sp.	0.2	2.3	2.5
Pterocarpus sp.	0.7	1.8	2.4
Ocotea argyrophylla Ducke	0.7	1.7	2.3
Inga sp. 1	0.8	1.5	2.3
Pouteria cuspidata (A.DC.) Baehni subsp. Dura (Eyma) T.D. Penn.	0.7	1.6	2.2
Protium aff. Subserratum (Engl.) Engl.	1.3	0.9	2.2
Pourouma sp. 2	0.8	1.3	2.1
Parkia velutina Benoist	0.8	1.3	2.1
Dendropanax caucanus (Harms) Harms	1.1	0.8	2.0
Licania sp. 1	1.5	0.5	1.9
Naucleopsis sp.	1.1	0.8	1.9
Minquartia guianensis Aublet	1.1	0.7	1.8
Virola elongata (Bentham) Warb.	1.1	0.7	1.8

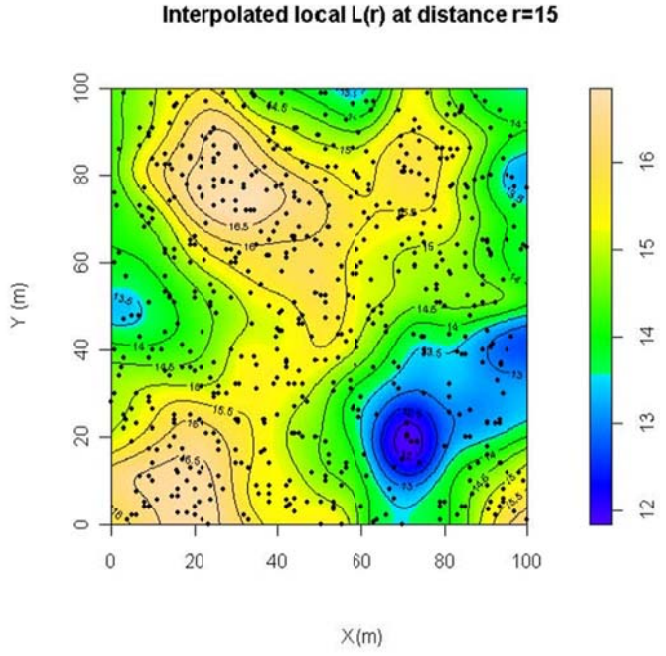
Cordia hebeclada I.M. Johnston	1.1	0.7	1.8
Nectandra cf. reticulata (R. & P.) Mez	0.7	1.1	1.8
Sapium sp. 2	0.2	1.6	1.7
Matisia malacocalyx (A. Robyns & S. Nilsson) W.S. Alverson	1.3	0.4	1.7
Brosimum utile (Kunth) Pittier subsp. Ovatifolium (Ducke) C.C. Berg	0.7	1.0	1.7
Tovomita weddelliana	1.0	0.7	1.7
Juyuintsa			
Oenocarpus bataua Mart. Burret	7.68	6.63	14.31
Iriartea deltoidea Ruiz & Pavón	7.20	4.63	11.83
Inga sp.	3.04	2.71	5.75
Parkia velutina Benoist	0.32	4.13	4.45
Himatanthus bracteatus (A. DC.) Woodson	1.28	1.72	3.00
Chrysophyllum pomiferum (Eyma) T.D. Penn.	0.48	2.48	2.96
Protium nodulosum Swart	0.96	1.76	2.72
Virola pavonis (A.DC.) A. C. Sm.	0.64	2.05	2.69
Matisia lasiocalyx	1.76	0.90	2.66
Apeiba membranacea Spruce ex Bentham	0.48	2.16	2.64
Guatteria sp.1	1.28	1.24	2.52
Virola aff. *sebifera* Aubl.	0.16	2.17	2.33
Guatteria sp. 2	1.44	0.85	2.29
Pachira punga Schunkei Fer. Alonso	1.28	0.91	2.19
Ocotea sp. 3	1.12	1.00	2.12
*Otoba parvifolia (*Markgr.) A. H. Gentry	0.64	1.46	2.10
Siparuna decipiens (Tul.) A. DC.	1.44	0.64	2.08
Guarea pterorhachis Harms	1.44	0.63	2.07
Chrysophyllum sp.	0.32	1.74	2.06
Clarisia racemosa R. & P.	0.80	1.21	2.01
Virola sp. 3	0.64	1.13	1.77
Sterculia tessmannii Mildbr.	0.48	1.17	1.65
Ocotea longifolia Kunth	0.96	0.68	1.64
Couropita sp.	0.16	1.43	1.59
*Pouteria caimito (*R. & P.) Radlk	0.32	1.27	1.59

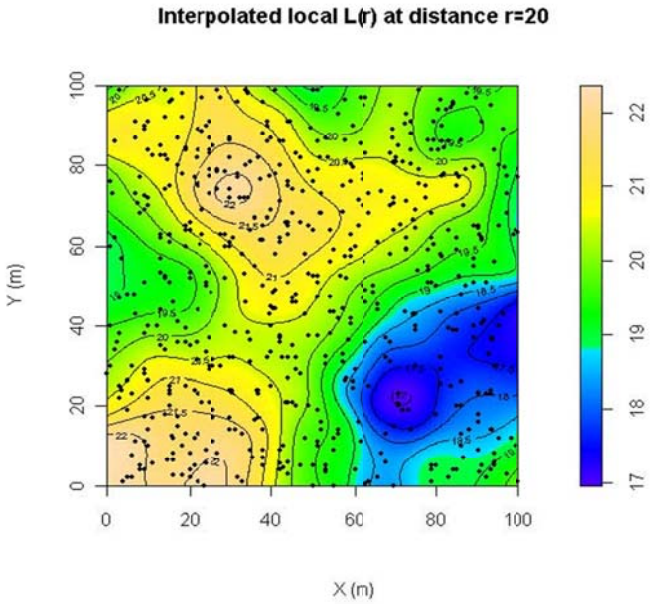
Virola flexuosa A.C. Smith	0.32	1.18	1.50
Couratari guianensis Aubl.	0.16	1.27	1.43
Sloanea cf. *Synandra* Bentham	0.16	1.24	1.40
Sterculia sp.	0.48	0.91	1.39
Guarea kunthiana A. Juss.	0.64	0.74	1.38

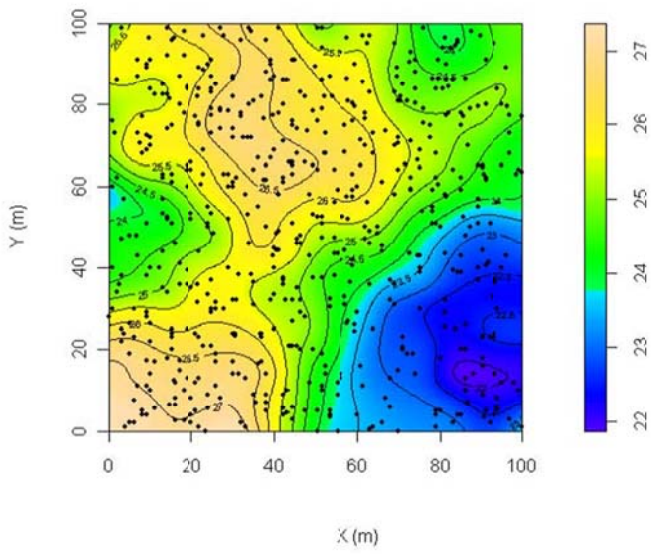
Appendix B

Local version ($L_i(r)$) of transformed Ripley's K (L(r)) that describes the overall spatial pattern at a particular distance r (Getis and Franklin 1987). The local $L_i(r)$ distribution at distance r = 10, 15, 20, and 25m in the tree inventory plot in Yutsuntsa is shown below.


Interpolated local L(r) at distance r=10
Y (m)
0
20
40
60
80
100
7
8
9
10
11
12


Interpolated local L(r) at distance r=15
Y (m)
X(m)
0
20
40
60
80
100
12
13
14
15
16


Interpolated local L(r) at distance r=20
Y (m)
X (m)
0
20
40
60
80
100
17
18
19
20
21
22


Interpolated local L(r) at distance r=25
Y (m)
X (m)
0
20
40
60
80
100
22
23
24
25
26
27

Appendix C

Part of tree inventory plot dataset from the three 1-ha plot data that contribute to international plot networks. For each plot only a sample of 30 individuals are shown.

Sawastian Family	Genus	Species	DBH(m)	Height(m)	Stratum
Mimosaceae	*Acacia*	*glomerosa* Bentham	14.4	10	Subcanopy
Mimosaceae	*Acacia*	*glomerosa* Bentham	44.7	40	Emergent
Mimosaceae	*Acacia*	*glomerosa* Bentham	55.5	50	Emergent
Mimosaceae	*Acacia*	*glomerosa* Bentham	67.0	30	Canopy
Mimosaceae	*Acacia*	*glomerosa* Bentham	50.1	40	Emergent
Mimosaceae	*Acacia*	*glomerosa* Bentham	52.5	45	Emergent
Euphorbiaceae	*Alchornea*	aff. *glandulosa* Poeppig	11.8	8	Understory
Euphorbiaceae	*Alchornea*	*triplinervia* (Spreng.)Mull. Arg.	12.6	12	Understory
Euphorbiaceae	*Alchornea*	*triplinervia* (Spreng.)Mull. Arg.	16.4	15	Understory
Euphorbiaceae	*Alchornea*	*triplinervia* (Spreng.)Mull. Arg.	22.5	15	Understory
Euphorbiaceae	*Alchornea*	*triplinervia* (Spreng.)Mull. Arg..	26.0	18	Subcanopy
Euphorbiaceae	*Alchornea*	*triplinervia* (Spreng.)Mull. Arg.	25.3	22	Subcanopy
Ulmaceae	*Ampelocera*	*longissima* Todzia	13.3	10	Understory
Ulmaceae	*Ampelocera*	*edentulata* Kuhlmann	69.0	40	Emergent
Tiliaceae	*Apeiba*	*membranacea* Spruce ex Bentham	20.4	12	Understory
Moraceae	*Batocarpus*	*orinocenses* H. Karsten	19.4	18	Subcanopy
Caesalpinaceae	*Bauhinia*	*arborea* Wunderlin	16.5	12	Understory
Lauraceae	*Beilschmedia*	aff. *pendula* (Sw.)Hemsl.	20.0	18	Subcanopy
Bixaceae	*Bixa*	*platycarpa* R. & P. ex G. Don	14.4	18	Subcanopy
Malphigiaceae	*Bunchosia*	*argentea* (Jacq.) DC.	20.4	15	Subcanopy
Malphigiaceae	*Bunchosia*	*argentea* (Jacq.) DC.	18.0	18	Subcanopy
Malphigiaceae	*Bunchosia*	*argentea* (Jacq.) DC.	13.7	12	Understory

Meliaceae	*Cabralea*	*canjerana* (Vahll.) Mart.	125.7	45	Emergent
Lauraceae	*Caryodaphnopsis*	*theobromifolia* (A.H.) van der Werff & H.G. Richt.	13.0	10	Understory
Euphorbiaceae	*Caryodendron*	*orinocense* H. Karst.	105.0	30	Canopy
Cecropiaceae	*Cecropia*	*herthae* Diels.	10.4	8	Understory
Cecropiaceae	*Cecropia*	*latiloba* Miquel	20.6	15	Understory
Cecropiaceae	*Cecropia*	sp.2	20.7	18	Subcanopy
Cecropiaceae	*Cecropia*	sp.2	23.0	15	Understory
Cecropiaceae	*Cecropia*	sp.2	37.0	30	Canopy
Yutsuntsa					
Rubiaceae	*Agouticarpa*	sp.	10.1	18	Subcanopy
Rubiaceae	*Agouticarpa*	sp.	25.2	25	Canopy
Ulmaceae	*Ampelocera*	*edentulata* Kuhlmann	22.6	28	Canopy
Euphorbiaceae	*Aparisthmium*	*cordatum* (Juss.) Baillon	13.3	11	Understory
Tiliaceae	*Apeiba*	*membranacea* Spruce ex Bentham	11.1	15	Understory
Arecaceae	*Astrocaryum*	*chambira* Burret	22.0	22	Canopy
Lauraceae	*Beilschmiedia*	*pendula* (Sw.) Hemsl.	10.8	10	Understory
Lauraceae	*Beilschmiedia*	*pendula* (Sw.) Hemsl.	11.1	12	Subcanopy
Lauraceae	*Beilschmiedia*	*pendula* (Sw.) Hemsl.	14.4	11	Understory
Hippocastanaceae	*Billia*	*rosea*	38.0	30	Emergent
Hippocastanaceae	*Billia*	*rosea*	21.2	20	Canopy
Moraceae	*Brosimum*	*lactescens* (S. Moore) C.C. Berg	13.0	12	Subcanopy
Moraceae	*Brosimum*	*utile* (Kunth) Pittier subsp. *ovatifolium* (Ducke) C.C.	14.0	7	Understory
Moraceae	*Brosimum*	*guianense* (Aublet) Huber	10.0	9	Understory
Moraceae	*Brosimum*	*guianense* (Aublet) Huber	10.3	8	Understory
Moraceae	*Brosimum*	*rubescens* Taubert	56.4	38	Emergent
Moraceae	*Brosimum*	*utile* (Kunth) Pittier subsp. *ovatifolium* (Ducke) C.C.	24.0	29	Canopy
Moraceae	*Brosimum*	*lactescens* (S. Moore) C.C. Berg	29.3	18	Subcanopy
Moraceae	*Brosimum*	*guianense* (Aublet) Huber	34.0	30	Canopy
Moraceae	*Brosimum*	*utile* (Kunth) Pittier subsp. *ovatifolium* (Ducke) C.C.	18.5	13	Understory
Moraceae	*Brosimum*	*utile* (Kunth) Pittier subsp. *ovatifolium* (Ducke) C.C.	50.5	30	Emergent
Caesalpinaceae	*Brownea*	sp.	10.7	9	Understory
Caesalpinaceae	*Brownea*	sp.	30.9	30	Emergent

Caesalpinaceae	*Brownea*	*grandiceps* Jacquin	16.7	15	Canopy
Combretaceae	*Buchenavia*	sp.1	16.0	12	Understory
Combretaceae	*Buchenavia*	sp.2	14.5	17	Understory
Malpighiaceae	*Byrsonima*	*putumayensis* Cuatrecasas	12.3	11	Canopy
Malpighiaceae	*Byrsonima*	*putumayensis* Cuatrecasas	19.6	16	Understory
Malpighiaceae	*Byrsonima*	*putumayensis* Cuatrecasas	16.9	12	Subcanopy
Myrtaceae	*Calyptranthes*	sp.	11.5	12	Subcanopy
Juyuintsa					
Mimosaceae	*Acacia*	*glomerosa* Benth.	54.7	40	Emergent
Mimosaceae	*Acacia*	*glomerosa* Benth.	10.4	16	Understory
Verbenaceae	*Aegiphila*	sp.	13.6	11	Understory
Arecaceae	*Aiphanes*	sp.	24.8	8	Understory
Euphorbiaceae	*Alchorneopsis*	*floribunda* (Benth.) Mull.Arg.	35.5	18	Subcanopy
Caesalpinaceae	*Andira*	*inermis* (W. Wright) Kunth ex DC.	20.2	17	Subcanopy
Annonaceae	*Annona*	*duckei*	10.6	12	Understory
Tiliaceae	*Apeiba*	*membranacea* Spruce ex Bentham	12.7	12	Understory
Tiliaceae	*Apeiba*	*membranacea* Spruce ex Bentham	84.9	30	Emergent
Tiliaceae	*Apeiba*	*membranacea* Spruce ex Bentham	31.5	20	Canopy
Arecaceae	*Astrocaryum*	*chambira* Burret	24.7	25	Canopy
Arecaceae	*Astrocaryum*	*chambira* Burret	14.2	10	Understory
Moraceae	*Batocarpus*	*orinocense* Karts.	23.2	17	Subcanopy
Moraceae	*Batocarpus*	*orinocense* Karts.	24.5	25	Canopy
Moraceae	*Batocarpus*	aff. *orinocense* H. Karts.	10.4	12	Understory
Moraceae	*Brosimum*	*acutifolium* Huber	19.8	15	Understory
Caesalpinaceae	*Brownea*	*grandiceps* Jacq.	10.8	12	Understory
Caesalpinaceae	*Brownea*	*grandiceps* Jacq.	16.3	12	Understory
Caesalpinaceae	*Brownea*	*grandiceps* Jacq.	12.5	10	Understory
Caesalpiniaceae	*Brownea*	*grandiceps*	15.2	12	Understory
Caesalpinaceae	*Browneopsis*	*ucayalina* Huber	10.6	6	Understory
Caesalpinaceae	*Browneopsis*	*ucayalina* Huber	10.2	12	Understory
Caesalpinaceae	*Browneopsis*	*ucayalina* Huber	14.5	15	Understory
Caesalpinaceae	*Browneopsis*	*ucayalina* Huber	11.4	8	Understory

Malpighiaceae	*Bunchosia*	*argentea* (Jacq.) DC.	32.0	17	Subcanopy
Malpighiaceae	*Bunchosia*	*argentea* (Jacq.) DC.	14.1	12	Understory
Malpighiaceae	*Bunchosia*	*argentea* (Jacq.) DC.	10.2	7	Understory
Malpighiaceae	*Byrsonima*	*putumayensis*	28.7	20	Canopy
Myrtaceae	*Calyptranthes*	sp.1	10.0	13	Understory

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Vita

Yung-Ho Ophelia Wang grew up in Taipei, Taiwan. Ophelia developed an interest in backpacking, assisted graduate students to conduct ecological studies of plots of the Center for Tropical Forest Science (CTFS) network during her undergraduate study, and received a BS in botany from National Taiwan University. With a strong interest in the Neotropics, Ophelia began her MS thesis work at the University of Illinois on how palms impose recruitment limitation on seedlings at La Selva Biological Station in Costa Rica and on Barro Colorado Island in Panama. A growing interest in applied ecology, conservation, and GIS motivated Ophelia to shift her MA work to Neotropical palm communities in fragmented forests in northern Costa Rica. Ophelia entered the PhD program at the University of Texas in 2005. Ophelia became an avid New York style salsa and Argentine tango dancer, as well as a devoted Couchsurfing member in graduate school. Currently she works as a Research Associate (Remote Sensing Scientist, Ecologist) at Northern Arizona University on a project that involves non-native plant invasions, fire risk, and wildlife habitats in the Sonoran Desert using remote sensing data. Ophelia hopes to continue contributing to biodiversity conservation studies using GIS and remote sensing information.

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